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MIXED-SPECIES GAME RANCHING ON THE ATHI PLAINS, KENYA

by

ⓒ J. BRAD STELFOX

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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Abstract

Ecological and production relationships were explored on an experimental game ranch in Kenya. The goals of Wildlife Ranching and Research Ltd. (WRR) are to demonstrate the environmental and economic wisdom of land-use systems based on commercial consumptive use of native ungulates.

A harvest technology emphasizing night-lighting of free ranging wildlife and on-Ranch processing of carcasses proved effective. Following government inspection, carcasses were sold to a strong domestic market. Dressing percentage, carcass shrink, body composition and external measurements were quantified to estimate potential revenue and determine the effects of a cropping program on morphometrics. Favorable growth in ungulate populations (12%/yr), despite an annual harvest of 40%, was attributed to a game proof fence preventing emigration, reduced cattle numbers, predator control and a skewed sex ratio favoring females.

Resource availability and utilization studies identified occupational patterns of native ungulates. Topographic relief and seasonal rainfall emerged as primary determinants of resource use largely through their affects on forage quality and quantity, although ungulate mobility and thermoregulation may have been important. Distinctive resource use patterns of Thomson's gazelle, Grant's gazelle, Coke's hartebeest and wildebeest ensured a level of ecological separation and encouraged balanced utilization of forages.

Prescribed burns improved rangeland quality in valleys for grazers by removing moribund vegetation and discouraging tree growth. High ungulate densities were recorded on all topographic levels of recently burned areas, presumably in response to a uniform sward of rapidly growing grasses.

Although comprising a small proportion of WRR, rangeland proximal to livestock enclosures (bomas) significantly affected distribution of native ungulates. Enriched by excreta, these biophysically distinct areas were characterized by increased grass productivity, utilization and quality. Relocation of bomas could be used by management to attract herbivores to underutilized rangelands.

Body condition of gazelles, measured by perinephric fat, fluctuated seasonally in response to forage quality. Dissimilar occupational patterns of Thomson's and Grant's gazelle accounted for their non-synchronic changes in body fat. Knowledge of weight gain and attrition would allow harvestors to concentrate on species with most favorable carcass characteristics.

Comparisons of morphometric measurements indicated that territorial male gazelles were older, heavier and possessed longer horns than bachelor conspecifics. Selective harvest of males on WRR has reduced competition among males for breeding females. To minimize inbreeding, a maximal sex ratio limit should be recognized and males from surrounding rangelands should be periodically introduced into the resident population.

As a management strategy, fenced game ranching appeared practical and economic under current conditions. However, the high capital investment required by this production system may preclude its development in other semi-arid regions. Another system of cropping wildlife is proposed as a practical and cost-effective alternative.

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Chapter 1

Introduction

1.1 Environmental Dilemma

Food production in Africa has become a focal issue. The severe plight of such Sahelian countries as Ethiopia, Sudan and Chad has only recently exposed the magnitude of this problem to western civilizations. High temperatures and insufficient rainfall preclude cereal crops from most of the continent's 32 million km^2 of rangeland, requiring food systems which emphasize meat production from domestic ungulates. Cattle, sheep and goat, which evolved in southwest Asia and were domesticated between 6,000 - 8,000 year b.p. (Mason, 1984), first appeared in sub-Saharan Africa appproximately 1200 years ago (Epstein and Mason, 1984). To ensure the survival and productivity of domestic species inhabiting unfavourable environments, extensive human provisioning has been required. Common practices/facilities include inoculations against disease, shelters, acaracides, water boreholes and the removal of competing wild herbivores and selected predators.

The impact of livestock on semi-arid ecosystems has led to their implication in environmental changes of continental proportions. The introduction of rinderpest by cattle in the 1880's led to a pandemic die-off among Africa's ungulates, with mortalities in excess of 90 percent reported for such species as wildebeest, buffalo and cattle (Sinclair, 1977). Pastoral and nomadic people such as the Masai, whose livelihood and spiritual welfare revolve around cattle, were decimated in numbers and distribution. Periodic epizootics continued until the early 1960's, when widespread immunization of cattle effectively prevented re-infection of wildlife. The greatest impediment to further cattle expansion in Africa is their susceptibility to trypanosomiasis, a disease transmitted by the tsetse fly. Unsuccessful attempts to control trypanosomiasis, which does not affect most indigenous ungulates, have resulted in the eradication of wildife and tsetse habitat over vast areas. Dasmann (1964) reported that 700,000 wild animals were killed in southern Rhodesia alone in a futile effort to eliminate the "fly".

Although unquantified, millions of Africa's wild herbivores are undoubtedly killed each year to reduce competition for water and forage with cattle. Not all deaths can be attributed to shooting; the modification of plant communities to benefit cattle has drastically reduced the amount of habitat available to wildlife.

A consensus exists among rangeland ecologists that abusive livestock grazing systems are impairing, if not destroying, the stability and productivity of Africa's grasslands. The impact of this man-induced process, when viewed over decades, may dwarf the episodes of rinderpest and the tsetse control programmes. The process of desertification has been identified by United Nations (UNCOD, 1977) as the major threat to the world's arid and semi-arid rangelands. Vast areas that once supported healthy, though fragile plant communities have deteriorated sufficiently to be unsuitable for wildlife, livestock or people. According to some estimates (Brown, 1974), desertification is responsible for the southward expansion of the Sahara by 45 km each year. The impact of drought on desertification cannot be overstated. Yet, by inducing such trends as reduced herbaceous cover, accelerated erosion, extensive tracking and exhausted water supplies, livestock have been a major contributor to the problem (Glantz, 1977).

New and enlightened approaches to food production are needed to ensure the survival of Africa's developing countries. Land use managers must examine the ecological and economic consequences of traditional livestock practices. A burgeoning human population and decaying resource base will soon demand such a re-evaluation. This is not to deny the importance of the livestock industry to Africa's future. Indeed, cattle are deeply rooted in the religious and social framework of many tribes, and will persist for this reason alone. Rather, land managers are challenged to recognize the limitations of conventional livestock, and to encourage herds only in those areas where environmental quality can be maintained. In arid settings, new resource-compatible technologies must be developed. Without healthy rangelands, unscarred by erosion, overutilization and reduced herbaceous cover, comparisons of alternative landuse systems become merely an academic exercise.

1.2 New Approaches to Meat Production

Recently, agencies such as the International Union for the Conservation of Nature (IUCN), United Nations Environmental Programme (UNEP) and World Wildlife Fund (WWF) have focused considerable attention on a global conservation strategy which emphasizes appropriate technologies and sustainable utilization of natural resources. Consistent with these objectives is the evaluation of "wild" ungulates as possible foundations for new meat industries in Africa. This view originated in the 1950's with such European and American biologists as W.H. Pearsall, F.F. Darling, H. Matthews and E.B. Worthington (Dasmann, 1964) and has been propagated more recently by Payne (1963), Talbot et al. (1965), Crawford (1972), Asibey (1974) and Hopcraft (1980). These researchers contend that sustained harvest of Africa's large and diverse wildlife populations could alleviate a widespread deficiency of protein in human diets. Though of historical and current importance to subsistence economies, the commercial role of wild ungulates has been largely overlooked. Since traditional livestock represent only a small percentage of the earth's 200 species of ungulates, it is not surprising that other species might prove useful as commercial meat producers. Current global examples of consumptive commercial use include red deer in New Zealand (Yerex, 1982), reindeer in Fennoscandia (Scotter, 1965), bison in North America (Peters, 1984) and a variety of native species in southern Africa (Skinner, 1973). Thorough reviews of the ecological and socio-economic basis for game ranching in Africa have been compiled by Walker (1979) and Field (1979).

Unlike livestock in Africa, indigenous species and their ancestral stock evolved under local environmental conditions during the past several million years. This prolonged co-evolutionary history has facilitated a high level of adaptation at the plant/animal interface. The physiological and ecological merits of indigenous ungulates have been presented as arguments for harvesting game to augment local meat supplies and earn foreign exchange (Field, 1974, 1979; Talbot, 1963; Skinner, 1970). Advantages of native ungulates often used to support this view include high fecundity and earlier sexual maturity (Skinner, 1971), lower water requirements (Taylor and Lyman, 1967; Taylor, 1968), resistance to disease (Karstad, Grootenhuis and Mushi, 1978), favorable carcass characteristics (Talbot et al., 1965) and more balanced resource use patterns (Lamprey, 1963; Ferrar and Walker, 1974).

In addition to the agricultural incentive, one of the main motivations for commercial utilization of game has been to direct benefits of wildlife conservation to landowners, thus obviating their replacement by livestock and dryland crops. By benefiting from the economic rewards of sustained consumptive use of wildlife, an incentive would exist for landowners to encourage both wildlife and their natural environment. Presently, wildlife are perceived by agriculturalists as competitors with livestock for food or as reservoirs of disease. Attempts to relieve these conflicts have resulted in wasted carcasses and have cost governments dearly in compensation and translocation programmes.

It has been claimed that production of game rather than livestock would minimize range degradation (Hopcraft, 1980; MILA, 1980), since a diverse assemblage of native ungulates would utilize a spectrum of forages (i.e. grasses, forbs, shrubs and trees). Low water requirements enable many xeric native species to forage distant from rivers, lakes and boreholes and to satisfy water requirements from hygroscopic plants. Confinement to night enclosures requires cattle to forage during daylight hours when heat load is greatest. Accordingly, the distribution of cattle is often restricted to the proximity of water holes during the dry season. These areas become severely over-utilized and characterized by reduced herbaceous cover and accelerated erosion.

Although the rationale of using wildlife may be sound, efficient and economic means for harnessing the productivity of wildlife present a challenge. Several systems, including game cropping, husbandry and ranching, have been attempted. Game cropping has been successful in response to management crises such as overpopulations of large herbivores in parks and reserves. The Kenya Wildlife Management Project (UNDP/FAO, 1980) developed a system for cropping plains game which was economic under prevailing price structures, but the project was terminated as a result of adverse public reaction.

The most intensive form of management, game husbandry using traditional methods for pastoral livestock production, has been explored by the Galana Game Domestication Project (King and Heath, 1976). Although the practicality of domestication has been demonstrated, many of the ecological advantages of wild herbivores are dissipated under close herding. Permits to market game products from Galana were rescinded in 1977 when the government suspended consumptive use of wildlife.

An intermediate strategy, game ranching on fenced holdings, incorporates the ecological advantages of essentially wild populations while maintaining the political necessity of controlling animal distributions and clarifying ownership. It is this category of consumptive use that this dissertation addresses.

1.3 Historical Review

In 1977, the Government of Kenya imposed a nation-wide hunting ban in an attempt to control rampant poaching, particularly of rhinoceros, elephant and large predators, and to provide sufficient time to devise effective controls for the sport hunting industry. A more effective strategy was needed to enforce hunting regulations, ensure redistribution of revenue to local landowners and prevent exploitation of wildlife by poachers and unethical sport hunters (MILA, 1980). This decision was strongly supported by such international conservation agencies as World Wildlife Fund and the International Union for the Conservation of Nature, who had invested considerable time and money toward ensuring a future for an international wildlife heritage held in trust by the people of Kenya. To the Kenyan economy, this decision sacrificed the badly-needed foreign exchange previously generated by sport hunting and removed a financial incentive for local people to conserve wild animals.

Although the reinstatement of big game sport hunting has not yet occurred, a single commercial game ranching venture has been operating since January 1981. Wildlife Ranching and Research Ltd. (WRR), owned by Dr. David Hopcraft, is a pilot project whose primary objective is to demonstrate the ecological and economic viability of semi-arid land use systems based on consumptive commercial use of indigenous ungulates. Following the completion of his doctoral research at WRR, Hopcraft (1975) concluded that communities of native ungulates were less damaging to the environment, more productive, required less water and veterinary attention, and possessed numerous carcass advantages over cattle. In 1977, Hopcraft applied to the Kenyan government for a permit to transform his existing cattle ranch into an experimental game ranching operation. In late 1980, Hopcraft received a permit and has to this date operated the only game ranch in Kenya.

WRR is the site of an ongoing inter-disciplinary study examining the ecological and socio-economic potential of game ranching in Kenya. Reed (1983) described the foraging strategies and digestive efficiencies of native and domestic ungulates. Bauer (1983) compared the economic performance of WRR to nearby cattle enterprises. The research project described in this dissertation was designed to complement the above studies and to address perceived gaps in the data base. Central foci of the study, which was conducted between May 1981 and August 1983, include detailing the technology of cropping wildlife, quantifying the harvest and numerical response of animal populations, documenting topographic-floral relationships, identifying resource use patterns of the economically important ungulates and exploring the managerial value of a prescribed burning program. It is the collective aim of projects conducted on WRR to provide information that can assist in effective resource management, for the future of this fledgling industry will depend largely on the establishment of a sound data set on which to base managerial decisions.

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Chapter 2

Environmental Setting

2.1 Location

The landholdings of Wildlife Ranching and Research Ltd. (8100 ha) are situated 40 km southeast of Nairobi, Kenya on the north-eastern limit of the Athi-Kapiti Plains (Figs. 2.1 and 2.2). Altitude varies between 1600 and 1700 m a.s.l., latitude is 01° 30' south and longitude is 37° 02' east. WRR is located immediately south of the major highway connecting the capital Nairobi to the coastal city Mombasa. The proximity of WRR to Nairobi and a major transportation artery has proved beneficial to the marketing of game products.

Rangeland located south of WRR in the Kajiado District is inhabited by Masai pastoralists. Members of the Wakamba tribe cultivate cereal and fruit crops in the Mua Hills to the north-east of WRR.

2.2 Climate

Although the factors controlling weather in East Africa are not fully understood (Griffiths, 1969), most observers attribute seasonal weather patterns to the existence of the Inter-Tropical Convergence Zone (ITCZ). This low pressure area marks the confluence of the northeast and southeast trade winds. The position of the ITCZ shifts with solar orientation, crossing the equator twice each year. This movement imparts a bimodal rainfall pattern to WRR.

Climatic observations were made at a central compound within WRR. Precipitation was monitored by three rain gauges while shade temperature and relative humidity were measured by a hygrothermograph housed within a Stevensen screen. Evaporation of water within rain gauges was prevented by a thin layer of kerosene.

Precipitation is characterized by considerable year to year variation. The long rainy season typically occurs from March to May, followed by a cool, cloudy and dry period from

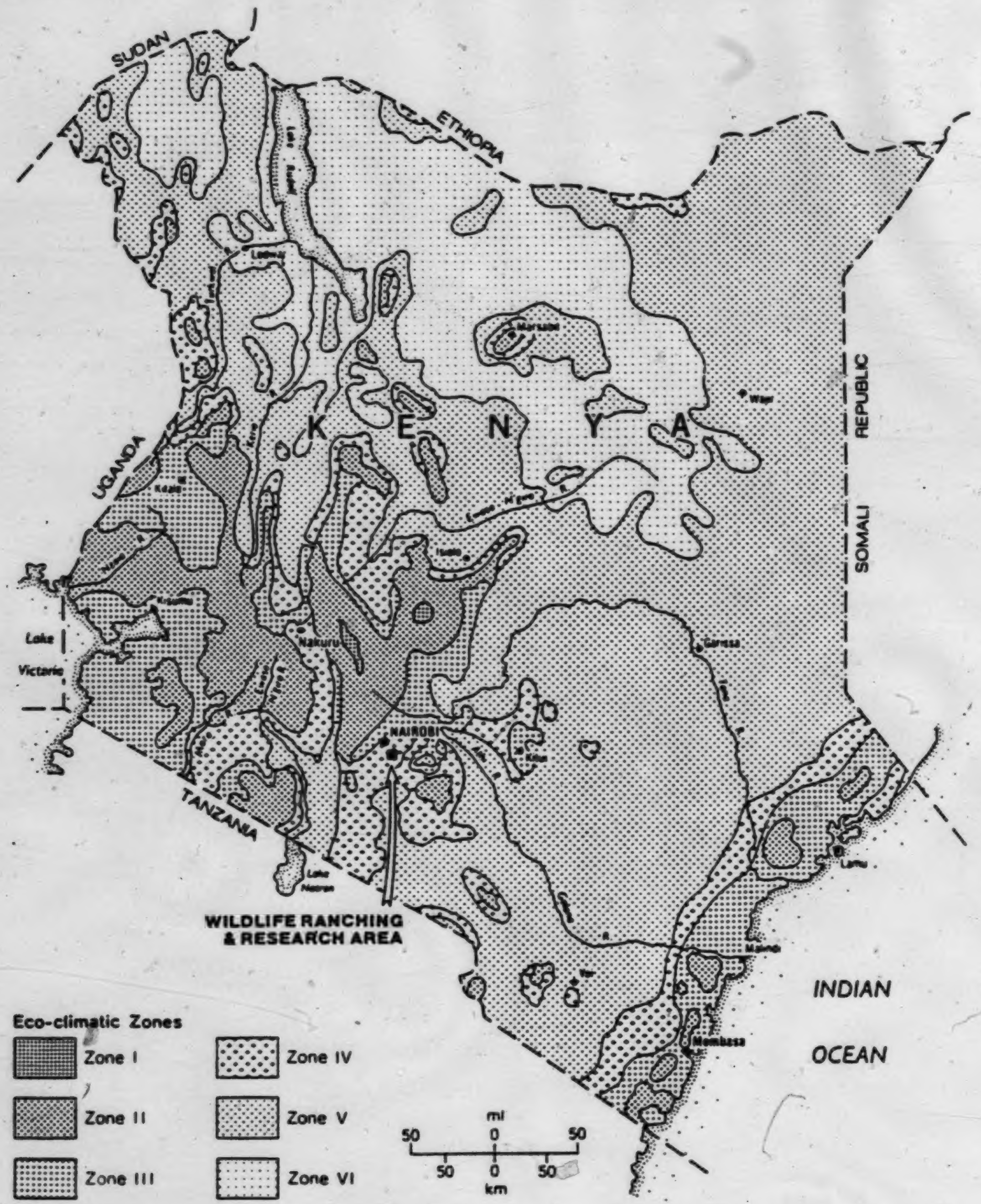

Figure 2.1 Ecoclimatic zones of Kenya, indicating location of Wildlife Ranching and Research Ltd. (modified from Pratt and Gwynne, 1977). Zone 1(Afro-alpine climate), Zone II (Tropical climate), Zone III (Dry sub-humid to semi-arid), Zone IV (Semi-arid), Zone V (Arid), Zone VI (Very arid).

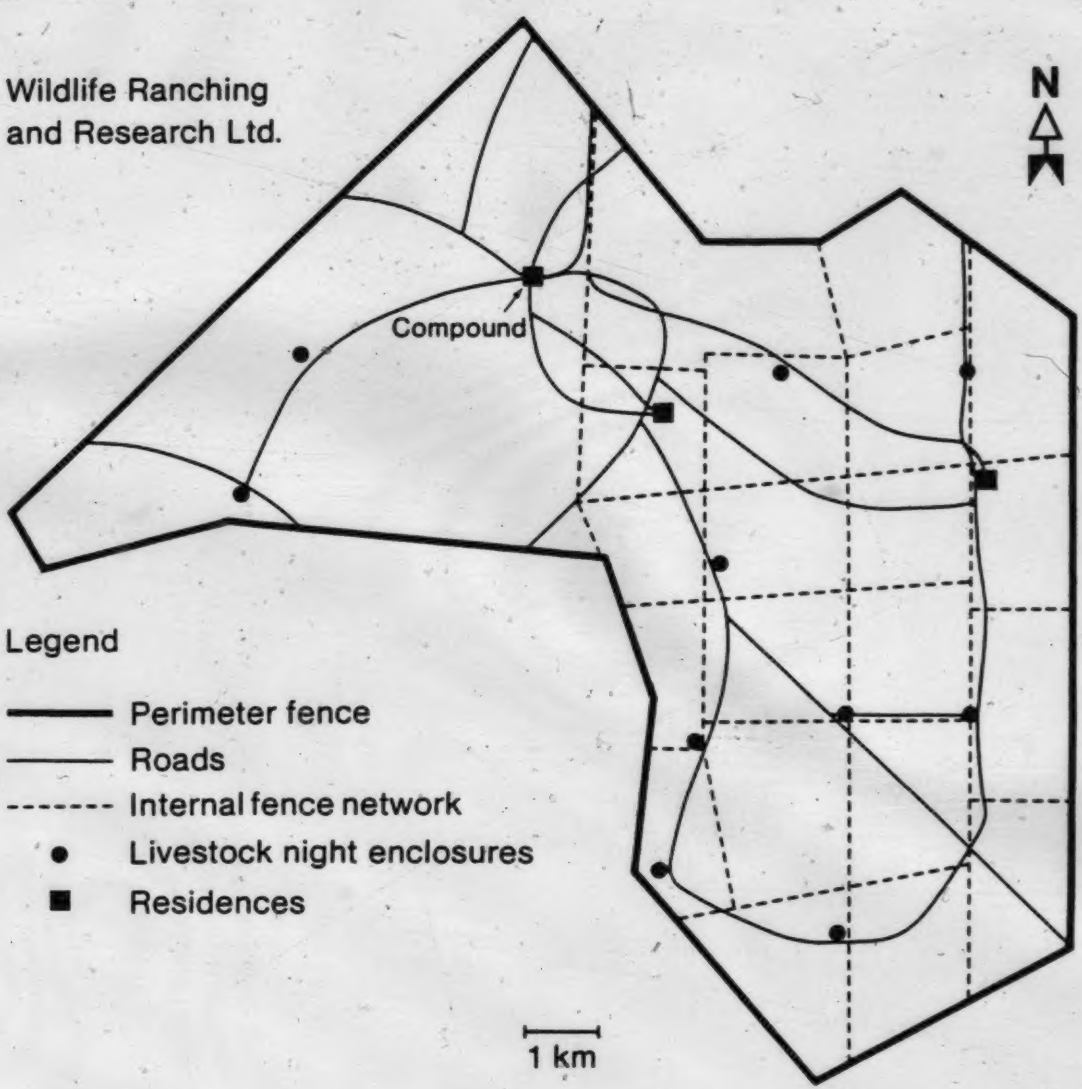

Figure 2.2 Map of WRR.

June to the end of September. The short rains occur from October through December and are followed by heat and intense sunshine from late December to mid-March. Average annual precipitation at WRR is 510 mm; although 422, 473 and 435 mm were received in 1981, 1982 and 1983, respectively. Rainfall patterns for 1981-1983 approximated historic bimodal patterns, although the long rains of 1982 and 1983 were light. Potential evapotransporation is 1500-2000 mm (Pratt and Gwynne, 1977), creating a water deficit for plants during much of the year. Monthly rainfall, humidity and temperature recorded at WRR are presented in Fig. 2.3. Highest temperatures and greatest daily range between maxima and minima occurred in February and March. Average annual maximum, minimum and mean annual temperatures at nearby Athi River over a 33 year period are 26.5, 14.1 and 20.3°C (E.A.M.D., 1970).

2.3 Geology

A review of East African geology is provided by Saggerson (1969). The landform of WRR and surrounding regions is the product of two geologic events. The hills Lukenya and Kyumbi which border WRR to the north and east and mark the border between the Plains and the Mua Hills were formed during a period of uplifting and folding in the Precambrian. The Athi-Kapiti Plains originated in the Tertiary and consist of volcanic deposits. Basalt rocks visible along topographic depressions evidence their volcanic origin.

2.4 Topography and Soil

Gently rolling terrain (slopes less than 2%) is the prevalent land form of WRR and the Athi-Kapiti Plains in general, although an interlace of riverine depressions periodically interrupts this pattern. By affecting water runoff and soil particle distribution, these undulations create a predictable toposequence of soil types, or "catena" (Morison, Hoyle and Hope-Simpson, 1948; Banage and Visser, 1967). Within WRR, eluvial soils along hilltops are sandy, well drained and light grey in appearance (Reed, 1983). Depressions are characterized by poorly drained black clay illuvials. The dominant soils are vertisols whose constituents are

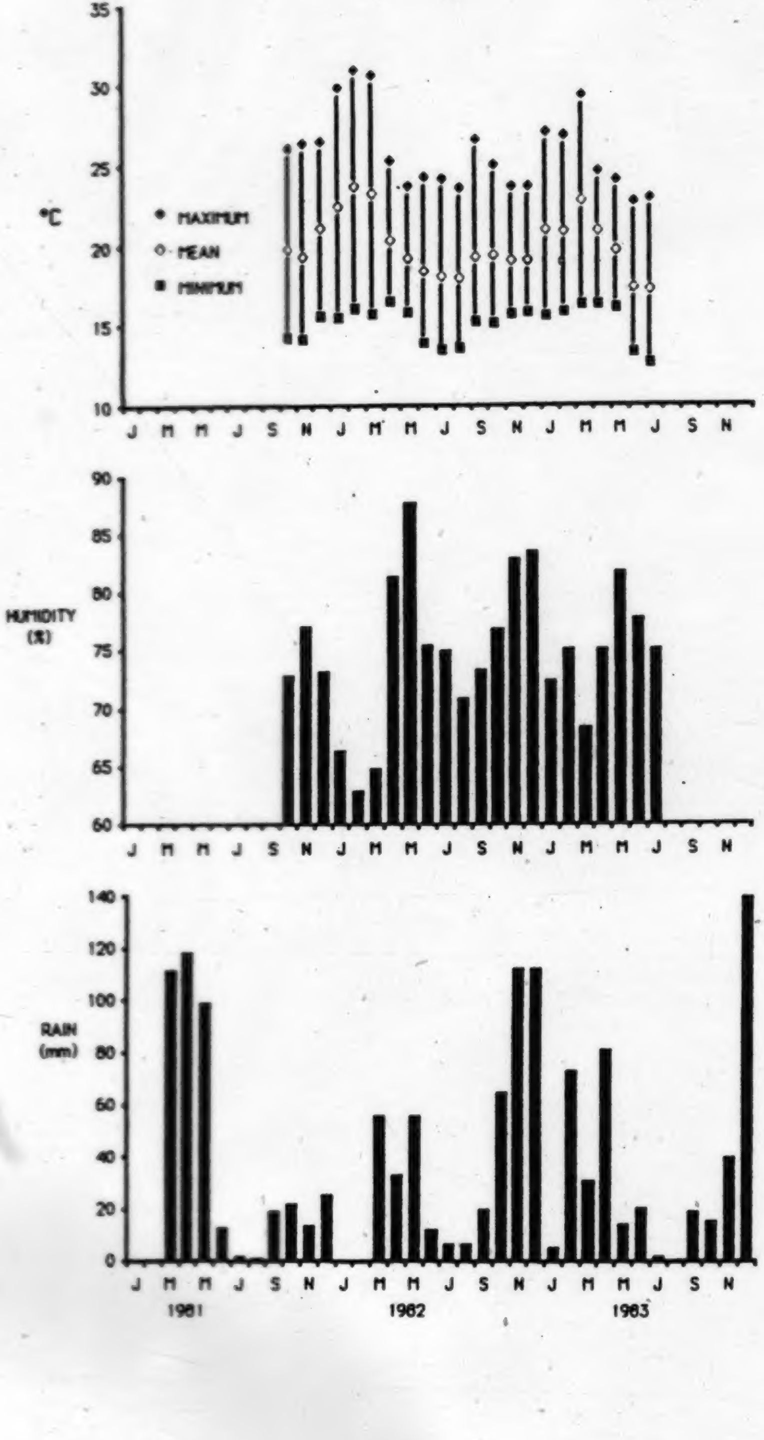

Figure 2.3 Meteorological summary.

primarily montmorillonite clays. These "black cotton" soils are poorly drained, swelling when hydrated and cracking when dry. Plant nutrients, other than nitrogen, are adequately supplied by the soil (Kuria, 1973).

2.5 Vegetation

The ecology and classification of East African vegetation are described by Edwards and Bodgan (1951) and Lind and Morrison (1974). According to Pratt and Gwynne's (1977) ecoclimatic classification, WRR falls into the Zone IV *Themeda-Acacia* association (Fig. 2.1), and therefore is representative of the more productive rangeland of Kenya. However, insufficient and unpredictable rainfall limits the potential for cultivated crops in this semi-arid region. The prevalence of "black cotton" soils on WRR greatly impede tillage.

Wooded grassland is the most common plant community in WRR, with topographic relief strongly influencing local species composition, leaf height, phenological stage and tree density. Chapters 4 and 5 describe the relationships between topography and plant community structure in greater detail. Dominant grasses are *Themeda triandra* Forsk., *Pennisetum mezianum* Leeke and *Digitaria milanjiana* Staph. The most prevalent trees are *Acacia drepanolobium* Sjoestedt, 1-2 m in height, in the valley bottoms and *Balanites glabra* Mildbr. and Schlect (2-4 m) along the ridges. A thin band of riverine vegetation is located along an ephemeral stream in the northern portion of WRR. This riparian region is characterized by a closed or semi-closed canopy forest of *Acacia xanothophloea* Benth., *A. senegal* Willd. and *A. seyal* Oliv. Botanical surveys of WRR conducted by Reed (1983) indicate that 242 species from 42 families are present. Most species belong to the families Gramineae (n=62), Papilionaceae (n=20), Compositae (n=19), Mimosaceae (n=13) and Malvaceae (n=12).

Ecoclimatic classifications of vegetation in East Africa are generally based on large scale gradients in topography, climate, vegetation and soil moisture. This scheme would be inappropriate for WRR as it would be unable to distinguish different regions within the relatively small ecoclimatic gradients present. In selecting a system for habitat classification, several requirements were considered.

1. The system should allow for quick visual assignment of areas into habitat classes. This would be especially important during road surveys when detailed inspection is not possible initally.
2. To incorporate the findings of the study into future management of WRR, rapid classification of habitat by staff is needed.
3. The categories should have a biophysical basis to enable meaningful interpretations of ungulate-habitat associations.
4. The classification should conform to an internationally accepted scheme.

Although graminoids comprised the greatest biomass and diversity of WRR's vegetation, it was not possible to base a classification on occurrence of these species. The vast majority of graminoids were distributed widely across gradients in topography, soil type and moisture.

It was possible to identify habitats using the criteria of occurrence and density of tree species. This scheme shares the same physiognomic criteria recommended by the East African Range Classification Committee (Pratt, Greenaway and Gwynne, 1966). Since trees are conspicuous features, rapid classification is facilitated. Strong habitat-ungulate associations (Chapter 4) indicate the ecological value of this classification system. Table 2.1 lists the classification criteria and briefly describes each habitat type. Figure 2.4 illustrates the relationship between topography and habitat distribution.

WRR was mapped into habitat classes by traversing north-south transects, viewing from topographic promontories and by studying 1981 aerial photographs (Fig. 2.5).

The results of topographic-floral studies (Chapter 4) suggest strong relationships between habitat types and topographic position, and therefore support the concept of catenas. Treeless Grassland and *Balanites* Grassland predominated in the upper topographic section, *Balanites-Acacia* Grassland favored the lower two sections and *Acacia* Woodland was restricted

Table 2.1. Definitions of habitat types on WRR.

Habitat	Area (ha)	Criteria	General Description
Treeless Grassland	227	Trees absent or sparse (0-2/ha)	-Restricted to hilltops -Grass leaf height low -Utilization high -Sandy well-drained soils
Balanites Grassland	2138	*Balanites* present (3-20/ha); *Acacia* absent	-Common along upper slopes -Grass leaf ht. low to medium -Utilization medium to high -Soils sandy-silt
Balanites-*Acacia* Grassland	3654	Both *Balanites* (3-20/ha) and *Acacia* (1-150/ha) present	-Lower and middle slopes -Leaf ht. high -Soils silt-clay -Utilization medium-low
Acacia Woodland	1458	*Acacia* present (>150/ha); *Balanites* absent	-Topographic depressions -Tree density high -Tall grass sward, utilization low -Poorly drained clay soils, which may be rocky
Riparian	584	Partial or complete canopy forest	-Stream .proximity -Characterized by dense stands of *A. xanthophloea seyal* and *senegal*
Fertile	39	Immediate vicinity of bomas. Trees absent or sparse	-Grass community dominated by *Cynodon* spp. -Soil fertility and util. high

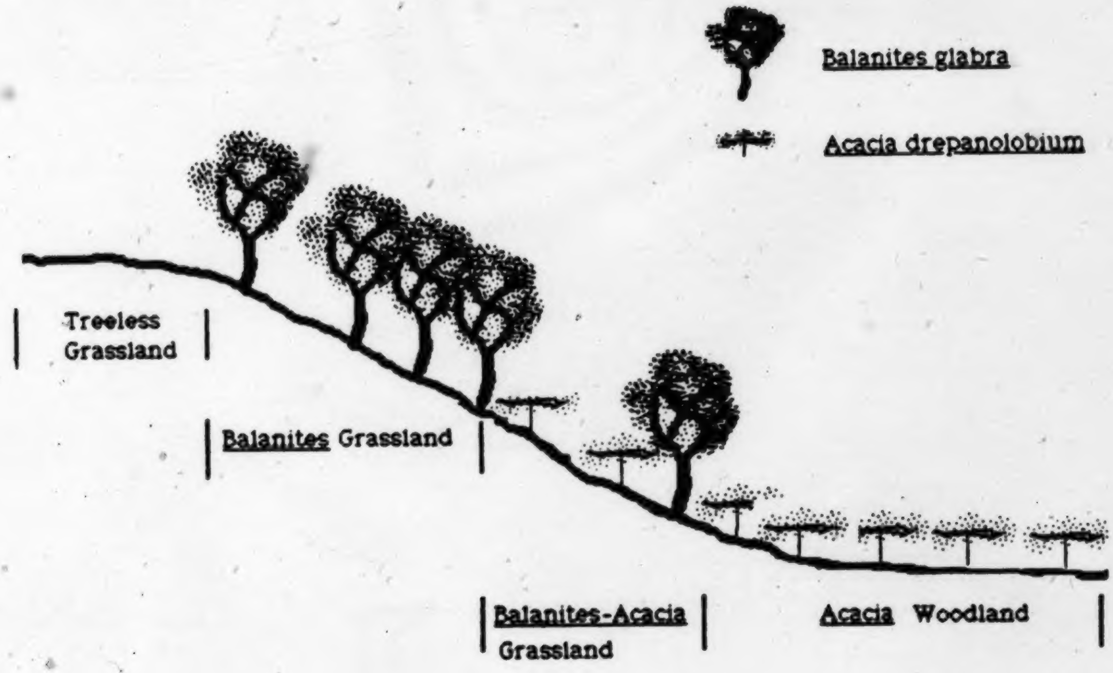

Figure 2.4 Relationship between topography and habitat distribution.

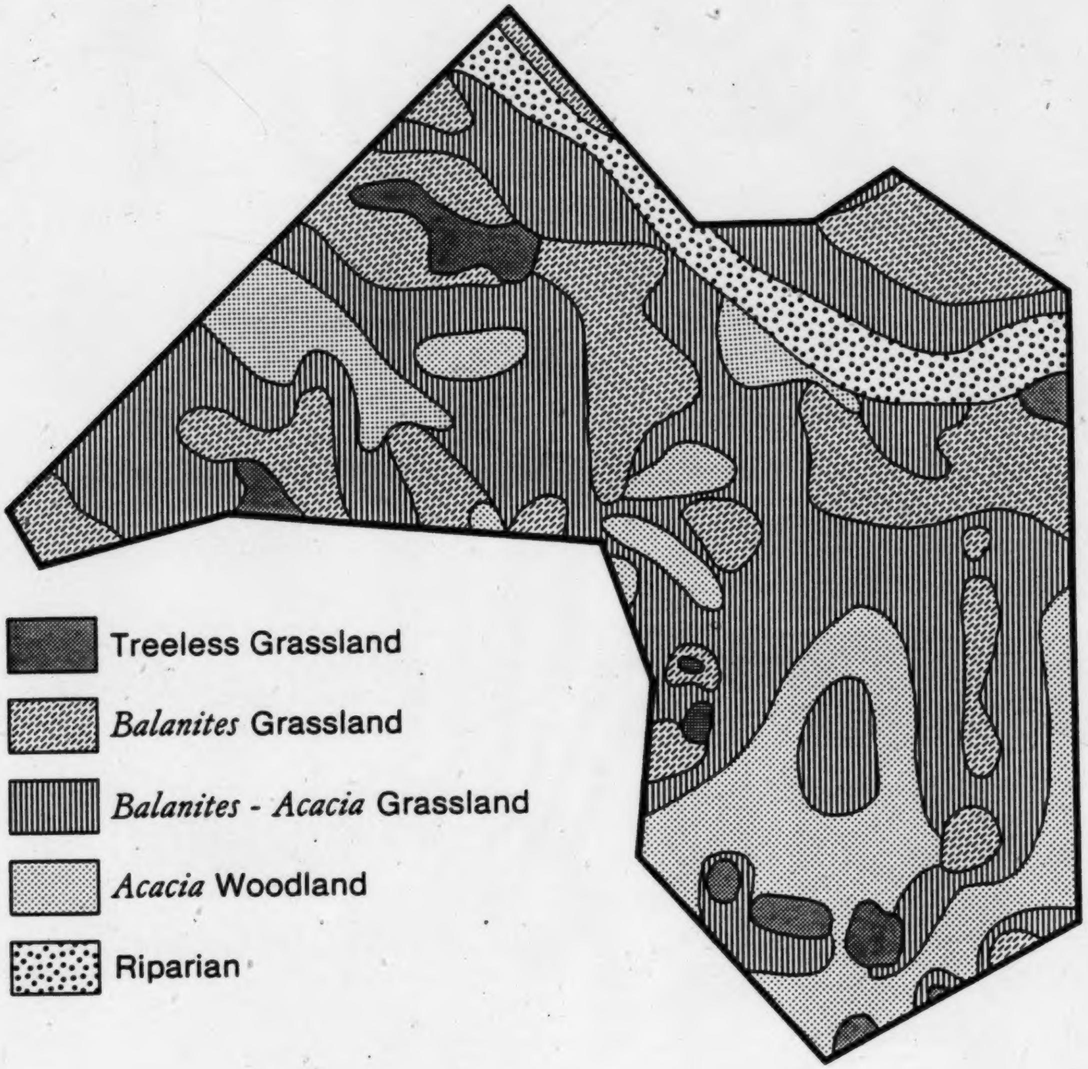

Figure 2.5 Habitat map of WRR.

to the lowest topography.

2.6 Fauna

Prior to 1981, WRR was operated as a livestock enterprise producing cattle (*Bos indicus*) and fat-rumped black-headed Somali sheep (*Ovis aries*). WRR presently supports a diverse fauna which features numerous indigenous ungulate species. Economically important are Thomson's gazelle (*Gazella thomsonii* Gunther), Grant's gazelle (*Gazella granti* Brooke), Coke's hartebeest (*Alcelaphus buselaphus* Gunther) and wildebeest (*Connochaetes taurinus* Burchell). Less numerous species include impala (*Aepyceros melampus* Lichtenstein), eland (*Taurotragus oryx* Pallas), Burchell's zebra (*Equus burchelli* Gray), Masai giraffe (*Giraffa camelopardalis* L.), fringed-eared oryx (*Oryx oryx* Ruppell), common duiker (*Cephalophus grimmia* L.), warthog (*Phacochoerus aethiopicus* Pallas) and steinbok (*Raphicerus campestris* Thunberg).

Predators including cheetah (*Acinonyx jubatus* Schreber), spotted hyena (*Crocuta crocuta* Erxleben) and black-backed jackal (*Canis mesomelas* Schreber) occur on WRR as resident populations, whereas lions (*Panthero leo* L.) and packs of hunting dogs (*Lycaon pictus* Temminck) periodically pass through the Ranch. Although not quantified, predation of gazelles is thought to be high. A predator control program exists on WRR for jackal, hyena and lion.

Other commonly seen mammals are the mongooses (*Mungos mungo* Gmelin, *Herpestes ichneumon* L., *Ichneumia albicauda* Cuvier), jumping hare (*Pedetes capensis* Forster), Whyte's hare (*Lepus whytei* Thomas), aardvark (*Orycteropus afer* Pallas), vervet (*Cercopithecus aethiops* L.), zorilla (*Ictonyx striata* Perry), and lesser galago (*Galago senagalensis* St. Hilaire).

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Chapter 3

Harvest, Population Dynamics and Morphometrics

3.1 Introduction

Localities where indigenous ungulates are harvested commercially in a systematic manner on a weekly or monthly basis are rare in East Africa. Even fewer facilities exist which collect a spectrum of morphometric data on each harvested animal. As commercial interest in the consumptive use of native ungulates grows, so does the need for detailed information concerning harvest strategies, cropping mechanics and productivity parameters. These data are required to devise effective management policies, to conduct economic comparisons with livestock species, to design appropriate processing facilities and to estimate retail biomass.

The objective of this chapter is to summarize knowledge gained at WRR during the first three years of conversion of a livestock ranch to a game ranching enterprise. In addition to quantifying the harvest (number, liveweight and carcass weight), other productivity parameters such as dressing percentage, carcass shrink and weight of blood, skin and edible offal were determined. The results of total ground counts were used to monitor the effects of the cropping regime and a skewed sex ratio on population dynamics. Morphometric measurements provide evidence of the effects of cropping on age structure.

3.2 Methods

3.2.1 Management Features and Capital Conversion

To meet government regulations for game ranching, WRR completed several modifications. A 50 km chain link fence, 2.6 m in height, was erected along WRR's perimeter at a 1977 construction cost of US $100,000. The fence serves to clarify ownership of wildlife and ensure a closed system for management. It has proven effective for all species except eland, whose exceptional jumping abilities make containment difficult. Weekly horseback patrols check the fence for damage and theft.

A slaughterhouse was constructed at a centrally located compound. An electrical winch is used to lift the larger animals from the killing vehicle to be suspended from a rail system attached to the ceiling. A diesel powered forced air cooling unit (2x2x5 m) is used to chill carcasses. Connected to the slaughterhouse is a meat processing room, equipped with mincer, presses and ovens for the production of mince, sausage, biltong and select meat cuts. A smoke house and open air drying rooms were constructed for the production of sausage and biltong.

Cropping is conducted from two specially modified 4-wheel drive vehicles, each equipped with a gun rest, mechanical hoist and a 2 way radio to allow drivers to relay information on animal distribution, hunting success and possible problems.

Internal postlines without wire, the remnants of an old paddocking system, occur in the eastern portion of the Ranch. During 1981 to 1983, approximately five livestock enclosures (bomas) were used nightly to protect cattle and sheep. Boma locations are changed periodically to avoid excessive trampling by livestock. Most management activities, human residences, and veterinary services occur at a centrally located compound. The undesirable features of "black cotton" soil during the rainy seasons have required human residences, bomas, boreholes and most roads to be located along ridges. Five boreholes, powered by either diesel engines or windmills, draw sufficient amounts of aquifer water to satisfy livestock and human requirements. Several dams have been constructed in depressions to trap surface flow of water during rainy seasons. These dams become dry for at least part of the year.

3.2.2 Harvest Strategy

During 1981, WRR managers attempted to adhere to a weekly harvest regime of 4 Thomson's gazelle *Gazella thomsonii*, 3 Grant's gazelle *Gazella granti*, 2 Coke's hartebeest *Alcelaphus buselaphus*, and 1 wildebeest *Connochaetes taurinus*. This ratio was sometimes disrupted by shifts in buyer demand, weather and irregularities of animal distribution. The establishment of the above harvesting ratio was intended to reflect species-specific fecundity and population levels, and result in sustained or enhanced future offtake. Harvest rates in 1982 and 1983 were adjusted for each species in response to data collected from ground counts.

Nearly all animals cropped in 1981 were adult males belonging to bachelor herds. The strategy was to selectively remove excess non-breeding males, thereby increasing the population's reproductive potential. By mid-1982, bachelor gazelle males were noticeably rare, requiring shooters to concentrate more on territorial males. It was not until late 1982 that females appearing "barren" were harvested in appreciable numbers to restore a less skewed sex ratio.

3.2.3 Harvest Protocol

Cropping occurs once weekly, usually Tuesday, to accomodate peak consumer buying on Friday. All harvesting is conducted at night using two specially adapted vehicles. Animals are immobilized with a spotlight and shot in the head to ensure immediate death and prevent meat spoilage. Gazelles are shot with a .22 Hornet, whereas a .243 or .308 caliber rifle is used for the larger species. Once shot, animals are hung immediately from the side of the cropping vehicle and exsanguinated. In accordance with meat hygiene standards, all animals are transported within one hour of being shot to the slaughterhouse, where they are eviscerated and skinned. Dressed carcasses are hung overnight for cooling.

The following morning, a government official inspects the carcasses and organs for disease and parasites that may render meat unsuitable for human consumption. Following inspection, meat is stamped to identify WRR as wholesaler and placed in a forced-air cooler for 24 hours of chilling. Since November 1981, meat from the forequarters of wildebeest and hartebeest has been boned and processed into sausage, mince or biltong (dried meat similar to jerky). Specialty meats, hindquarters of the larger species, and entire carcasses of gazelles are marketed to select butchers and restaurants in Nairobi. Meat is covered by cheesecloth, placed in an insulated box, and transported by truck. The time interval between harvesting and delivery of meat to retail market is approximately 36 hours. Edible offal is sold primarily as pet food. To date, no hides or horns have been sold. They are in storage awaiting government permission to export.

3.2.4 Total Ground Counts

Populations of commercial species were monitored by monthly ground counts. WRR was divided into 4 or 5 sectors, with each area counted simultaneously by 1 or 2 experienced observers. Counts were conducted by four-wheel drive truck or motorcycle between 0600 and 1000 h to minimize heat wave visibility problems. Viewers observed the entire sector, either by close inspection or by using binoculars from vantage points. It was necessary to remain distant (>200 m) from wildebeest and hartebeest, to minimize inter-sector movement of frightened animals. Using this census technique, visibility bias in open woodland is thought to be low for large-bodied gregarious species, whereas uncounted animals present a greater problem for cryptic species occurring in small groups. While conducting ground counts, sex was distinguished only among adult gazelles, since they were more noticeably dimorphic and were more easily approached than hartebeest and wildebeest. However, it was not possible to distinguish the sex of young gazelles. Age classes were distinguished for hartebeest and wildebeest on the basis of coat colour and horn conformation changes.

3.2.5 Morphometrics

A variety of limb, trunk and horn measurements, described in Table 3.1, are completed when animals arrive at the abbatoir. Following evisceration, the heart, liver, lungs, kidneys and spleen are weighed. In addition, several other morphometric parameters were quantified. Blood was collected in the field from 10 headshot animals for each of the four economic species. Subsequently liveweights were determined by applying a blood loss correction factor to bled weights. To estimate sale value of hides, generally determined by surface area, 20 air-dried salted hides from each species were measured for length, width and weight. Carcass shrink for the period beginning at evisceration and ending at time of delivery (36 hours later)

Table 3.1. Description of morphometric measurements.

Measurement	Description
Head length (cm)	From tip of nose to the atlas joint measured along the dorsal curvature of the head.
Body length (cm)	From atlas joint to base of tail, measured above vertebral column.
Shoulder height (cm)	Measured from highest point on the withers to tip of hoof following the curves of the shoulder when extended straight.
Hind height (cm)	Measured from the base of the tail along the body curves of the hindleg to the hoof tip while leg is extended.
Horn length (cm)	Between base and tip of the horn measured along frontal surface.
Tip to tip (cm)	Distance between horn tips.
Base circumference (cm)	Measured around the base of the horn.
Liveweight (kg)	Predicted weight of living animal, determined by applying a blood loss correction factor to the recorded bled weight.
Carcass weight (kg)	Refers to eviscerated carcass with head, skin and lower legs removed.
Perirenal fat (g)	That adipose tissue surrounding the kidneys. It was necessary to separate perirenal fat from adjacent mesenteric deposits. In such cases, fat extending beyond the end of the kidney was removed.
Heart (g)	Heart proper removed from pericardium. Ventricles opened to remove clotted blood.
Lung (g)	Includes lungs and trachea
Liver (g)	Includes liver and gall bladder
Spleen (g)	Spleen only
Kidney (g)	Includes kidney proper (surrounding adipose tissue removed).
Organs (% of liveweight)	Cumulative weight of heart, liver, spleen, lungs and kidneys.
Head (% of liveweight)	Head proper including lower jaw, horn and skin covering severed from body at atlas-axis junction.
Lower legs (% of liveweight)	Portion of leg including skin and hoof removed at joint distal to ulna or tibia.
Gastro-intestinal content (% of liveweight)	Includes full digestive tract (oesophagus to anus) and contents.

was quantified for 30 carcasses of each species. A sample of fresh hides, gastro-intestinal tracts (contents included), head and lower legs were weighed in late 1982.

3.3 Results

3.3.1 Harvest Statistics

Table 3.2 summarizes harvest and production during 1981, 1982 and 1983. Over 500 individuals were harvested each year, producing an average annual yield of 43.7 tonne liveweight, 23.6 tonne dressed carcasses and 1,563 kg of edible offal. Average annual productivity over this period was 5.40 kg/ha liveweight, 2.92 kg/ha dressed weight and 0.19 kg/ha edible offal. As a proportion of the January biomass densities, the cropping rate for the economic species was 36.2, 44.6 and 40.2 percent during 1981, 1982 and 1983, respectively. The numbers of males and females in the harvest are shown in Table 3.2. Few females were cropped prior to September, 1982. An insignificant number of carcasses were condemned (Grant's gazelle less than 2%; other species less than 0.5%).

3.3.2 Population Dynamics

From January 1981 to January 1984, livestock biomass was progressively reduced from 86.3 to 44.4 kg/ha to encourage growth of native ungulate populations (Fig. 3.1). Between January 1981 and January 1984, economic native ungulates increased 35.8 percent from 12.0 to 16.3 kg/ha (Table 3.3). To standardize those environmental conditions (i.e. leaf height and colour) and life history events (i.e. calving season) which affect animal visibility and population levels, only January census figures were used to express population trends. Results of monthly total ground counts are presented in Figs. 3.2 and 3.3.

Wildebeest calves were born in April and May. Although neonates of Thomson's gazelle, Grant's gazelle and hartebeest were counted each month, rainy seasons were preferred for calving.

Table 3.2 WRR harvest statistics (1981-1983).

	Thomson's gazelle	Grant's gazelle	Coke's hartebeest	Wildebeest	Total
Male Harvest					
1981	243	150	84	32	509
1982	118	55	144	70	387
1983	128	48	135	80	391
Female Harvest					
1981	0	4	13	4	21
1982	27	33	42	38	140
1983	59	28	44	40	171
Total Harvest					
1981	243	154	97	36	530
1982	145	88	186	108	527
1983	187	76	179	120	562
Liveweight (kg)					
1981	5,643	8,949	12,592	7,912	35,096
1982	3,175	4,506	20,195	19,203	47,079
1983	3,665	4,043	19,046	22,236	48,990
Dressed weight (kg)					
1981	3,166	5,128	6,724	4,312	19,330
1982	1,781	2,573	10,663	9,928	24,945
1983	2,038	2,318	10,185	12,120	26,661
Edible Offal (kg)					
1981	218	347	373	229	1,167
1982	130	199	715	688	1,732
1983	168	172	689	764	1,791
Liveweight (kg/ha/yr)					
1981	.697	1.105	1.555	.977	4.334
1982	.392	.557	2.494	2.372	5.815
1983	.452	.499	2.351	2.745	6.048
Dress weight (kg/ha/yr)					
1981	.391	.633	.830	.533	2.387
1982	.220	.318	1.317	1.226	3.081
1983	.252	.286	1.257	1.496	3.291

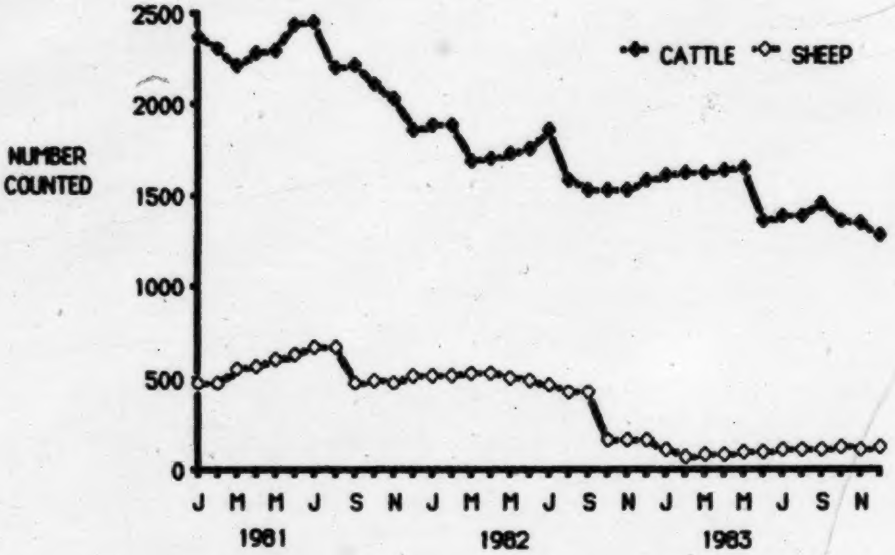

Figure 3.1 Livestock populations on WRR.

Table 3.3. Ungulate populations on WRR, January 1981 - January 1984.

	Average	January 1981		January 1982		January 1983		January 1984	
	Weight (kg)	N	Biomass	N	Biomass	N	Biomass	N	Biomass
WILDLIFE									
T. gazelle	16	622	9,952	555	8,880	727	11,632	970	15,520
G. gazelle	35	460	16,100	360	12,600	335	11,725	307	10,745
C. hartebeest	85	446	37,910	617	52,445	665	56,525	594	50,490
Wildebeest	125	264	33,000	253	31,625	335	41,875	445	55,625
Subtotal		1,792	96,962	1,785	105,550	2,062	121,757	2,316	132,380
Biomass (kg/ha)			12.0		13.0		15.0		16.3
LIVESTOCK									
Cattle	288	2,360	680,000	1,876	540,288	1,500	432,000	1,235	355,680
Sheep	40	475	19,000	503	20,120	150	6,000	91	3,640
Subtotal		2,835	699,000	2,379	560,408	1,650	438,000	1,326	359,320
Biomass (kg/ha)			86.3		69.2		54.1		44.4
TOTAL BIOMASS (kg)			795,960		665,958		559,757		491,700
(kg/ha)			98.3		82.2		69.1		60.7

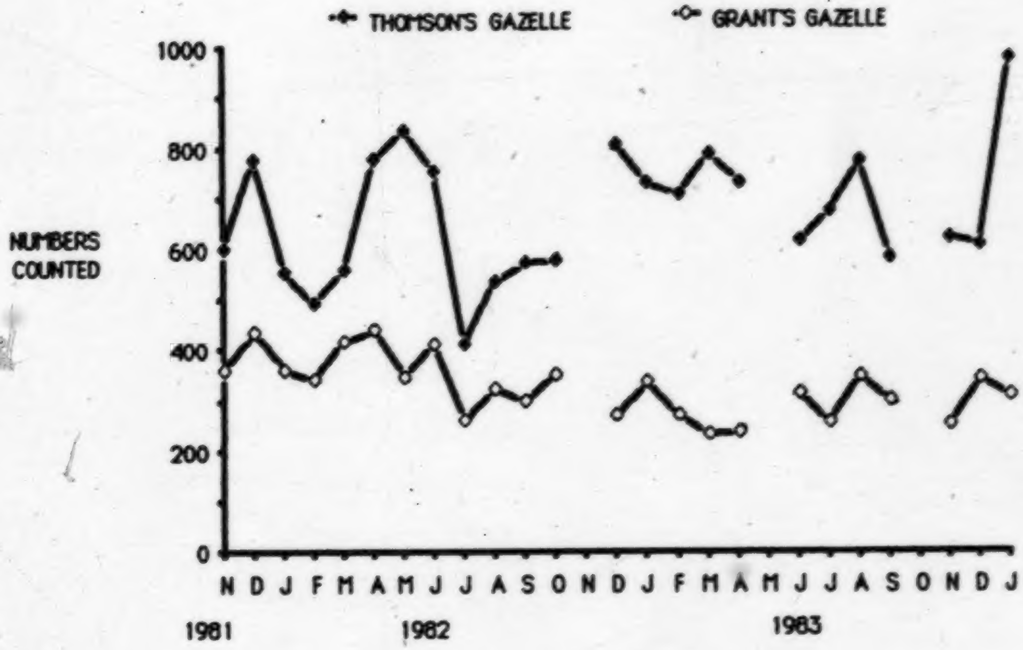

Figure 3.2 Populations of Thomson's and Grant's gazelle on WRR.

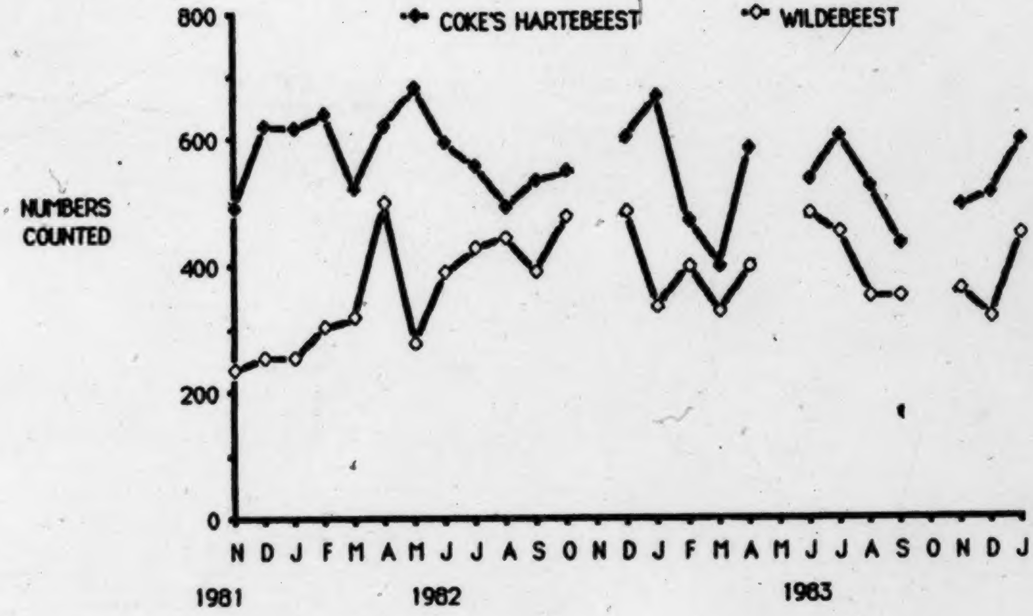

Figure 3.3 Populations of Coke's hartebeest and wildebeest on WRR.

The effects of a selective harvest of males, practiced between January 1981 and September 1982, are seen in the highly skewed sex ratio recorded for gazelles in the surveys (Fig. 3.4). Sex ratio figures relate all females and non-adult males to recognizable adult males (i.e. visibly long and/or thick horns).

Population levels for the currently unharvested species, as of January 1984, were 30 zebra, 20 eland, 75 giraffe, 75 impala and 11 fringedeared oryx. It was not possible to accurately count steinbok and warthog.

3.3.3 Morphometrics

Annual summaries, tabulated for both sexes, are presented for carcass and organ characteristics (Tables 3.4 and 3.5) and external measurements (Tables 3.6 and 3.7). Table 3.8 describes hides, carcass shrink and blood. Table 3.9 quantifies the contribution, expressed as a percentage of liveweight, of dressed carcasses, digestive contents, head, organs and skin.

During the 36 hour period between cropping and retail delivery, whole carcasses sustain evaporative weight losses of 2 to 5 percent. As depicted in Fig. 3.5 carcass shrink decreases with increased weight.

3.4 Discussion

Substantial quantities of meat (approximately 25 metric tonne/yr) were produced in a hygienic manner and marketed readily in Nairobi. The three year mean harvest of 5.4 kg/ha appears small in comparison to a fully stocked cattle ranch, which might harvest 25 kg/ha liveweight annually, livestock biomass on WRR during the period of study exceeded that of native species by a factor of three to seven. It is assumed that wildlife will expand greatly as the cattle population is further reduced.

The data indicate that dressed carcasses vary between 52 and 57 percent of liveweight and that females and larger-bodied species have lower dressing percentages. In comparison, dressing percentages of cattle on WRR are approximately 50-51 percent. As a proportion of

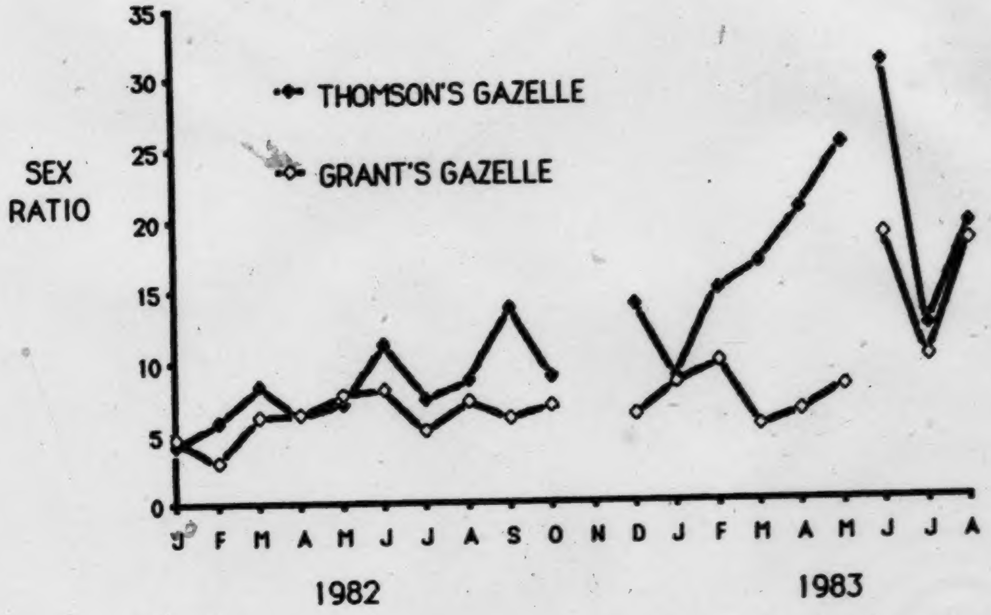

Figure 3.4 Gazelle sex ratio on WRR (ratio relates adult males to all other sex and age classes).

Table 3.4 Carcass and organ summaries of harvested males (all values represent monthly means, n=12 for 1981 and 1982, n=8 for 1983).

	Thomson's gazelles			Grant's gazelles			Coke's hartebeest			Wildebeest		
	1981	1982	1983	1981	1982	1983	1981	1982	1983	1981	1982	1983
Liveweight (kg)												
X	23.4	22.3	20.6	57.9	58.7	57.6	130.1	110.6	104.4	216.7	207.2	207.2
Carcass weight (kg)												
X	13.1	12.5	11.5	33.2	33.5	34.0	69.5	58.4	57.3	118.1	107.1	109.9
se	0.6	0.2	0.3	0.6	1.1	1.5	0.5	1.1	2.2	4.4	4.6	4.2
Dressing %												
X	56.1	56.1	55.8	57.3	57.1	59.0	53.4	52.8	54.5	54.5	51.7	53.0
Lungs (g)												
X	318	291	307	785	756	809	1296	1025	1178	2377	2034	2188
se	6	7	9	16	31	80	27	59	60	86	115	45
Heart (g)												
X	178	162	166	367	344	395	784	626	676	1211	1019	1110
se	4	6	5	11	14	21	24	20	35	65	47	49
Liver (g)												
X	278	269	272	754	672	847	1226	931	1127	1907	1884	1869
se	3	3	10	35	50	86	78	63	49	105	231	69
Spleen (g)												
X	98	89	105	214	194	250	440	378	427	544	482	522
se	4	4	2	8	10	12	16	19	14	39	33	34
Kidney (g)												
X	33	29	32	84	73	82	115	99	104	210	161	177
se	1	1	1	1	4	3	4	5	4	15	9	5

Table 3.5 Carcass and organ summaries of harvested females (1981-82 values are means of individual measurements, 1983 values represent monthly means).

	Thomson's gazelles		Grant's gazelles		Coke's hartebeest		Wildebeest	
	1981-82 n=27	1983 n=6	1981-82 n=35	1983 n=6	1981-82 n=55	1983 n=6	1981-82 n=39	1983 n=6
Liveweight (kg)								
X	17.4	18.4	42.3	41.3	91.0	107.8	140.2	156.8
Carcass weight (kg)								
X	9.7	9.6	24.3	23.9	47.4	54.8	73.6	82.7
se	0.3	0.1	0.5	0.4	1.4	2.9	3	5
Dressing %								
X	55.7	52.2	57.4	57.9	52.1	50.8	52.5	52.7
Lungs (g)								
X	245	283	635	628	1100	1228	1717	1828
se	8	6	39	54	43	76	61	78
Heart (g)								
X	141	144	271	312	579	620	757	943
se	4	3	8	18	22	23	32	67
Liver (g)								
X	236	273	575	627	951	906	1728	1540
se	9	9	32	30	44	63	62	66
Spleen (g)								
X	83	85	170	196	349	398	394	464
se	4	3	7	11	12	12	14	30
Kidney (g)								
X	28	29	60	70	88	110	145	150
se	2	1	2	2	4	6	6	6

Table 3.6. External measurement summaries of harvested males (all values (cm) represent monthly means, n=12 for 1981 and 1982, n=8 for 1983).

	Thomson's gazelles			Grant's gazelles			Coke's hartebeest			Wildebeest		
	1981	1982	1983	1981	1982	1983	1981	1982	1983	1981	1982	1983
Head length												
X	21.1	21.0	23.0	29.3	27.7	29.5	55.4	56.7	53.8	59.7	60.5	59.9
se	0.6	0.3	0.2	0.8	0.8	0.5	0.8	1.0	0.7	1.0	1.2	1.4
Body length												
X	79.0	78.1	74.3	106.3	106.9	103.9	121.7	116.7	116.2	134.2	129.3	128.7
se	0.5	0.7	0.9	0.8	1.3	1.0	1.3	0.9	1.6	1.6	2.1	1.8
Heart girth												
X	61.1	63.0	62.8	85.3	86.8	85.3	118.9	113.1	113.3	146.1	140.1	148.3
se	0.3	0.7	1.4	0.8	1.4	2.4	1.0	0.9	1.4	1.3	2.3	1.7
Shoulder height												
X	66.3	66.1	64.1	92.7	92.4	91.6	118.9	117.8	116.5	131.0	128.7	132.6
se	0.4	0.4	0.6	0.5	1.1	2.0	1.0	0.6	1.4	1.7	1.4	1.0
Hind length												
X	73.4	72.7	70.0	99.9	101.0	97.4	112.6	111.5	109.3	121.9	122.3	119.5
se	0.3	0.5	0.9	0.5	0.9	0.6	0.6	0.8	1.0	1.3	1.6	0.7
Horn length												
X	29.7	26.8	22.6	50.3	49.6	44.1	37.8	37.6	34.9	51.1	49.6	46.5
se	0.8	0.9	1.2	1.4	1.0	1.5	0.5	0.7	1.1	1.1	2.0	1.4
Tip-to-tip												
X	9.3	9.2	8.3	25.8	24.3	25.8	30.4	27.5	24.2	40.2	38.6	37.6
se	0.1	0.2	0.3	0.2	0.3	1.8	0.5	0.8	1.5	1.3	1.1	1.6
# of horn rings												
X	20.3	19.5	16.1	26.2	27.4	26.9	12.0	12.0	11.9	-	-	-
se	0.3	0.6	0.9	0.5	0.7	1.8	0.4	0.5	0.5			
Circ at base												
X	10.9	9.6	9.3	16.3	15.4	15.0	21.6	19.4	19.2	34.0	30.0	31.0
se	0.1	0.2	0.4	0.2	0.3	0.2	0.2	0.3	0.3	0.7	1.1	0.7

Table 3.7 External measurement summaries of harvested females (1981-82 values are means of individual measurements, 1983 values represent monthly means).

	Thomson's gazelles		Grant's gazelles		Coke's hartebeest		Wildebeest	
	1981-82	1983	1981-82	1983	1981-82	1983	1981-82	1983
	n=27	n=6	n=35	n=6	n=55	n=6	n=39	n=6
Head length								
X	20.3	21.6	26.6	27.9	50.4	48.7	56.8	52.8
se	0.2	0.5	0.5	0.3	1.1	2.1	1.0	1.3
Body length								
X	78.7	73.6	101.0	96.8	112.7	114.7	118.4	120.2
se	0.2	0.8	1.0	2.7	0.5	2.0	1.6	1.9
Heart girth								
X	64.5	63.2	78.9	86.2	106.5	117.1	131.0	138.0
se	0.6	1.8	0.8	5.6	1.5	3.2	1.9	4.7
Shoulder height								
X	64.4	64.2	86.0	86.3	111.8	115.5	119.3	123.6
se	0.5	0.9	1.8	2.0	1.2	1.5	1.7	1.3
Hind length								
X	69.8	68.5	94.8	91.0	107.5	110.8	112.8	113.3
se	0.5	0.6	1.4	1.4	0.9	5.2	1.0	0.4
Horn length								
X	7.3	8.7	26.0	25.6	30.1	30.7	36.9	37.4
se	0.6	0.7	0.2	1.2	0.8	1.0	1.1	1.3
Tip-to-tip								
X	4.8	5.9	12.8	13.3	22.5	26.2	29.9	31.3
se	0.1	0.1	0.2	0.7	1.0	3.0	0.9	3.8
# of Horn rings								
X	-	-	19.7	21.0	10.9	11.6	-	-
se			0.7	0.7	0.3	0.8		
Circ at base								
X	3.0	3.1	7.7	7.0	16.0	15.2	20.6	20.1
se	0.2	0.4	0.2	0.5	0.5	0.5	0.6	1.4

Table 3.8. Blood, carcass shrink and hides

	Thomson's gazelle	Grant's gazelle	Coke's hartebeest	Wildebeest
Blood (% of liveweight, n=10)				
X	3.47	3.19	3.45	3.32
se	.23	.22	.17	.21
Carcass Shrink (%, n=30)				
X	4.84	3.32	2.53	2.02
se	0.48	0.36	0.24	0.19
Hide Length (cm, n=20)				
X	91.8	129.4	148.7	150.1
se	0.9	1.3	1.6	2.5
Hide Width (cm, n=20)				
X	50.8	74.5	103.1	123.1
se	0.9	1.1	1.3	1.6
Hide Weight (kg, n=20)				
X	0.56	1.34	5.23	8.31
se	0.02	0.04	0.28	0.42

Table 3.9. Comparison of body composition by sex and species (% of liveweight).

	Thomson's gazelle		Grant's gazelle		Coke's hartebeest		Wildebeest	
	M (n=13)	F (n=16)	M (n=10)	F (n=11)	M (n=18)	F (n=10)	M (n=10)	F (n=10)
Digestive contents								
X	20.6	23.5	18.0	21.9	21.2	21.7	21.0	20.0
se	2.3	3.2	1.3	3.0	2.7	2.2	1.8	5.5
Lower Legs								
X	2.7	2.6	2.5	2.7	2.7	2.4	2.2	2.3
se	0.4	0.4	0.2	0.5	0.3	0.6	0.3	0.4
Head								
X	7.6	6.2	7.5	5.3	7.4	6.4	7.4	6.4
se	0.4	1.3	0.8	0.7	0.6	0.8	0.3	1.0
Organs								
X	4.4	4.7	3.8	4.7	3.7	3.6	3.0	3.4
se	0.4	0.9	0.8	0.7	0.4	0.6	0.4	1.0
Skin								
X	5.3	5.4	5.0	4.7	6.7	5.9	7.0	6.8
se	0.7	0.8	0.6	0.7	0.7	1.2	0.7	0.9
Dressed Weight								
X	56.9	51.9	58.1	57.3	54.1	50.7	51.0	48.3
se	3.6	5.3	2.3	6.4	2.3	4.4	3.5	2.9

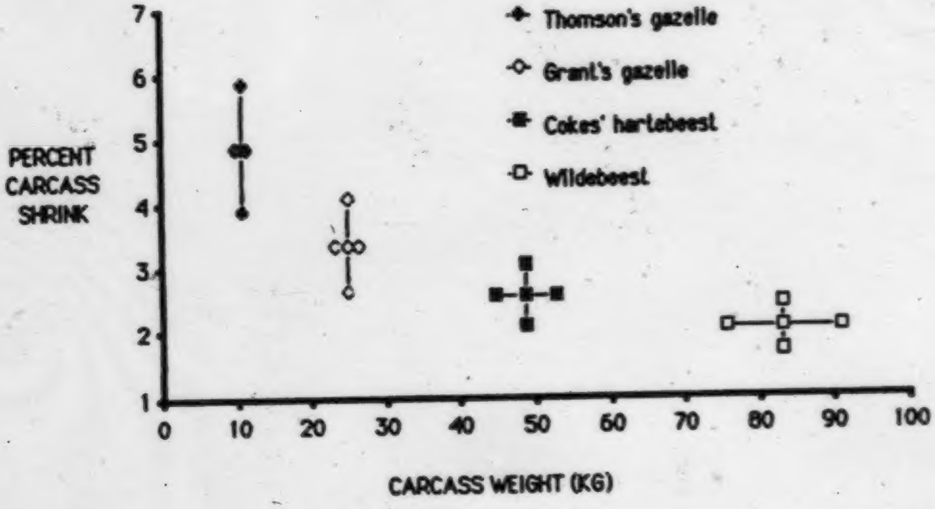

Figure 3.5 Percent carcass shrink during 36 hour period following evisceration.

liveweight, edible offal (heart, liver, lung, kidneys, spleen) amounts to approximately 3.4 to 4.7 percent. Percentages are higher for females and decline with increased body weight. Carcass shrink is attributable to a number of factors, including relatively small carcass size, lack of subcutaneous fat to form a protective sheath, and to the evaporating effects of a forced-air cooler. Expectedly, smaller carcasses sustain proportionately greater weight loss.

In comparison with observed growth rates of unharvested ungulate populations in East Africa, the performance of wildlife on WRR appears impressive. Following the removal of the rinderpest virus in the early 1960's from the Serengeti ecosystem, buffalo and wildebeest increased by approximately 10% annually for several years until limited by available forage (Sinclair, 1979). Within the nearby Mara ecosystem, populations of T. gazelles, G. gazelles and hartebeest exhibited maximum annual rates of increase of 45, 26 and 13%, respectively (Stelfox et al., in review).

Cumulatively, the biomass density of ungulate species on WRR increased by 12% annually while withstanding an annual harvest of approximately 40 percent. These data suggest an expansion rate in excess of 50 percent if harvesting had not occurred. Several explanations are invoked to account for the observed growth pattern. First, reductions in livestock populations have improved environmental quality by creating an abundance of forage and by lengthening the season of surface water availability. One would expect the attendant reduction in inter- and intraspecific competition to push fecundity to intrinsic maxima and to reduce mortality associated with poor body condition. Secondly, existing ungulate biomass densities of 16-20 kg/ha (including non-economic species) have been maintained well below carrying capacity by the harvesting regime. Sustainable biomass densities of 43.8 to 56.2 kg/ha (Petrides, 1956) and 122.6 kg/ha (Talbot and Talbot, 1963) have been reported on similar grassland of East Africa. In nearby Nairobi National Park, an area similar in environmental setting, yearly censuses indicated an average biomass of 46.2 kg/ha despite a livestock stocking rate of 10.7 kg/ha (Foster and Coe, 1968). Predictions of potential biomass density on WRR, based on rainfall/phytomass/ungulate biomass relationships (Coe, Cummings and Phillipson, 1976), are 35-45 kg/ha. Thirdly, the strategy of harvesting primarily males has increased the populations' growth potential by skewing the sex ratio in favour of females. For example, at a female:male ratio of 10:1, and assuming all adult females are serviced, population growth would double that of a sex-balanced population. Although only females which appeared "barren" were harvested, a high percentage were determined by post-mortem inspection to be in early stages of pregnancy. These findings suggest that conception rates can remain high when females outnumber breeding males by several magnitude. Fourthly, the construction of a game proof perimeter fence prevented the emigration of animals. Since intraspecific aggression should encourage emigration among adolescent and subordinate males (Leuthold, 1979), a barrier should increase animal density. Fifthly, WRR's predator control policy has greatly reduced populations of jackals and hyena. Jackals were thought to be a major limiting factor on gazelles by preying on neonates in the "hiding" stage. Lastly, counting efficiency of observers may have improved with experience. If this is true, earlier populations would be underestimated relative to more recent counts. This artifact would provide a misleadingly high estimate of population growth. Although improvements in observer performances have undoubtedly occurred, I believe its impact to be minor relative to the other considerations.

A three pool model (calves, juveniles and adults) was used to determine if WRR's ungulate community could increase as observed while sustaining the recorded harvest. First, the model credited females with maximal fecundity rates recorded in the literature since populations were low and were experiencing an unlimited food resource. Next, each population was subjected to an age and sex class specific harvest to reflect observed harvest figures. Finally, mortality rates were adjusted to produce a population increase consistent with results of ground censuses. The vital statistics used in the population simulation model are shown in Table 3.10. The results of the model are useful in elucidating the response of each species. Grant's gazelle differed from other economic species, in that their numbers decreased. The model indicates that natural mortality was much higher for G. gazelle than other species. Body condition studies (Chapter 7) indicate that G. gazelle were in good condition, offering no

Table 3.10. Vital statistics used in population dynamics model.

	Mortality Rate	Fecundity Rate[1]	Harvest Rate	Liveweight[2] (kg)
T. gazelle				
Calves	.15	0	0	13
Juv. Males	.12		0.6	20
Juv. Females	.12	1.5	0	16
Ad. Females	.08	2.0	0.15	20
Ad. Males	.08		0.6	25
G. gazelle				
Calves	.25	0	0	25
Juv. Males	.22		0.5	45
Juv. Females	.22	1.2	0	35
Ad. Females	.18	1.5	0.2	50
Ad. Males	.18		0.6	60
C. hartebeest				
Calves	.07	0	0	60
Juv. Males	.05		0	100
Juv. Females	.05	1.0	0	80
Ad. Females	.03	1.2	0.2	100
Ad. Males	.03		0.5	140
Wildebeest				
Calves	.03	0	0	80
Juv. Males	.02		0.6	150
Juv. Females	.02	1.0	0	120
Ad. Females	.01	1.0	0.1	150
Ad. Males	.01		0.6	200

[1] Maximal fecundity values are based on the literature review provided by Kingdon (1982). The author modified some of these values to reflect observed calving intervals on WRR.

[2] Liveweight measurements based on data collected at WRR.

justification for lowering fecundity. Although speculative, preferences of G. gazelle for lower topographic levels (Chapter 4) might predispose animals to predation because of high tree density and reduced traction in swollen clay soils. A more likely explanation concerns the diet of Grant's gazelle. Whereas the other 3 economic species and cattle relied primarily, or exclusively, on grasses, G. gazelle foraged extensively on dicotyledons (Chapter 4). Therefore, reductions in cattle numbers would not benefit G. gazelle to the same extent as the other species.

It was noted that economic native species, particularly males, became more wary of the cropping vehicle with passing time. The more gregarious species exhibited a greater flight distance than the gazelles. To cope with this problem, hartebeest and wildebeest were shot from greater distances with larger caliber rifles. No appreciable reduction in shooting accuracy was observed. If flight distances continue to increase, it may become necessary to implement a different harvesting strategy.

Total time required to shoot and process animals decreased significantly during the study period. Whereas approximately seven hours were required for 10 animals in early 1981, only 2-3 hours are presently needed. Greater efficiency can be attributed to improvements in labour expertise, vehicle reliability, processing equipment and slaughterhouse design.

Horn dimensions decreased between 1981 and 1983 for males of each species (Table 3.6). Since horn size is a useful indicator of age, one might conclude that the age structure is shifting toward younger individuals. This is not surprising, since shooters generally select large horned individuals. Age determination studies of 1982-83 male Thomson's and Grant's gazelle (Chapter 8), confirmed that "old" males did not exist on WRR. Interestingly, measures of skeletal dimensions and carcass size remained similar or did not decrease as noticeably (Tables 3.4 and 3.6). I suspect that improved environmental conditions, a result of declining livestock numbers, enabled young individuals to grow quickly.

3.5 Summary

WRR's performance demonstrates that game ranching is logistically possible. Recognizing that WRR is in an experimental phase, it is not surprising that cropping and processing systems are being modified to improve economic efficiency, meat quality and marketability. However, ultimate concerns about system performance must await enterprise maturity when livestock have been removed and wildlife have achieved optimal densities.

Perhaps the most encouraging result of the study was the ability of native ungulate populations to increase (12%/annually) while sustaining offtake rates of 35 to 45 percent. Management strategies which contribute to these findings include predator control, maintenance of a skewed sex ratio, improvements in environmental quality by reducing livestock and construction of a perimeter game proof fence. Maximal sustained offtake rates for cattle in the vicinity of WRR are 25% (Nsibandze, 1982).

Advantages of ranching indigenous species over cattle include higher fecundity, earlier sexual maturity, more balanced foraging patterns, greatly reduced veterinary costs, and lower water requirements.

Although less tangible than economic criteria, potential benefits to the environment resulting from game ranching should remain a most critical consideration. It is important to realize that the ecological and economic findings of this study are site and time specific. They reflect the conversion of a single beef ranch to a game enterprise. Other systems of game utilization will be more or less viable, depending on a number of ecological, economic, regulatory and marketing factors.

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Chapter 4

Dynamics of Resource Use by Ungulates on the Athi Plains, Kenya

4.1 Introduction

Partitioning of resources by sympatric species is well-established (Schoener, 1974). Studies of resource use have identified habitat cover (Harris, 1972; Hudson, 1976), topographic relief (Bell, 1970), proximity to water (Western, 1975), diet (Gwynne and Bell, 1968; Mugambe, 1982) and forage phenology (Vesey-Fitzgerald, 1960), among others, as critical environmental gradients along which ungulates achieve ecological separation. The capacity of herbivores to exploit dissimilar, often complementary, resources has been offered as an explanation for the spectacularly diverse ungulate communities of East Africa (Lamprey, 1963; Jarman and Sinclair, 1979).

The objective of this study is to apply the findings of resource partitioning studies to the management of an experimental land-use system where native ungulates are commercially harvested. It is postulated that sympatric ungulate species exhibit dissimilar preferences for forage and habitat, and that the dynamic nature of East African grasslands, largely the result of seasonal rainfall, necessitates flexibility in resource use patterns. Practical applications of revealed patterns would include 1) suggesting optimal combinations of herbivore species for existing resources, 2) identifying those resources receiving excessive and negligible use and 3) forecasting responses of ungulates to environmental changes induced by such management practices as prescribed burning. The usefulness of a habitat classification scheme for managing economically important ungulate species was also examined.

4.2 Methods

4.2.1 Ungulate Resource Use

Resource use patterns of Thomson's gazelle (*Gazella thomsonii*), Grant's gazelle (*Gazella granti*), Coke's hartebeest (*Alcelaphus buselaphus*) and wildebeest (*Connochaetes taurinus*) were monitored during wet (October 1982 - May 1983) and dry (September 1982, June - August 1983) seasons. Criteria used to distinguish seasons included monthly rainfall (Figure 2.3), soil moisture and plant phenological stage. Surveys were conducted twice monthly by motorcycle along a 34 km road encompassing all topographic levels and major non-riparian vegetation types. For each ungulate sighted within 200 m of the road, ocular estimates were made of selected floral and physical characteristics (Table 4.1). Ocular estimates were calibrated to objective step-point transects (Appendix 5.1) each month between September 1981 and August 1983. Ocular estimates required approximately ten minutes/site, during which time flora and ground cover located within 25 m of the site centre were considered. Each site was assigned to one of the habitat types listed in Table 2.1, then the distance to the nearest water body was measured using a detailed map.

4.2.2 Diet Determination

Botanical composition of diets was determined by microhistological faecal analyses. Two faecal collections were made for each species; the first during the rainy season (December 1982) and the second in the dry season (July/August 1983). Faecal material was collected from four individuals of each species during the wet season. Dry season sample consisted of 8 Grant's gazelle and 16 of Thomson's gazelle, hartebeest and wildebeest. Approximately 50 ml of faecal material were removed from the rectum of harvested animals, dried, then analyzed by M. Mugambe of Colorado State University using the techniques outlined by Williams (1969) and Ward (1970). Five slides were prepared from each faecal sample. Twenty fields/slide were examined microscopically, yielding a total of 100 fields per sample. A diet item was recorded if

Table 4.1. Description of biophysical variables.

Measurement *	Description
Ground Cover	
(Litter, Soil, Grass Shrub & Forb)	Percentage of ground cover, viewed aerially, that consists of each parameter.
Topo-Floral	
Leaf Height (cm)	Average height of grass leaves, including those on both flowering and vegetative tillers.
Phytomass (g/m^2)	Average air-dry weight of attached herbaceous vegetation, litter not included.
Utilization (%)	Percent of grass tillers exhibiting defoliation on tillers of the current year.
Tree Density (#/ha)	Number of Acacia drepanolobium and Balanites glabra counted within a 50 x 50 m area and multiplied by a factor of four.
Topographic Level	Topography divided into three levels (upper=1, middle=2, lower=3). Site estimated visually according to local drainage.
Distance to Water	Distance between animal sighting and surface water (dam or borehole), measured on a detailed map (1 cm=125 m).

* All measurements except tree density and distance to water determined by calibrations to objective step-point transects conducted before the study and continued throughout (see Appendix 5.1).

two or more identifiable characteristics were observed in a field. Plant identity was confirmed by comparing fragment characteristics to a reference collection.

An assumption of microhistological faecal studies is that the proportion at which various species are represented in egesta reflect the foraging habits of the animal. Although Todd and Hansen (1973) and Hansen, Peden and Rice (1973) contend that dissimilarities between ingested and egested mixtures are minor, Fitzgerald and Waddington (1979) and Skiles, Kortopates and Van Dyne (1980) argue that grass forages are over-estimated by this technique because they are more resistant to digestion than are dicotyledons.

4.2.3 Statistical Analyses

Multiple discriminant analysis (MDA) was used to determine underlying environmental gradients contributing to ecological separation. This multi-variate approach has been successfully employed in ungulate resource use studies by Ferrar and Walker (1974) and Hudson (1976). Environmental gradients which are most important in discriminating species (or habitat type) are identified by extracting orthogonal linear functions from the original data set. Canonical correlation coefficients quantify the relative importance of resource variables to each function. Although certain environmental variables may be shown by MDA to be important in discriminating herbivore species, these variables may not be sufficiently prevalent to maintain actual ecological separation. Therefore, a subjective interpretation of resource availability must accompany MDA analyses. Resource use patterns were visualized graphically as territorial maps which show species "centroids" (highest probability of relative dominance) and variance. These maps indicate habitat niche breadth and proximity of individual species and illustrate distinctiveness of habitat types. For comparing ungulate species, data collected from road surveys (topographic-floral distribution) and faecal analyses (diet) were analysed separately. Dietary data are expressed as a percent of total observations and have been arc-sin transformed to improve homoscedacity.

Analysis of variance was also performed on all environmental variables to determine differences in inter-specific resource use and habitat type.

4.3 Results

4.3.1 Environmental Gradients

The impact of topographic relief on plant community structure was dramatic. Proceeding downhill, tree density, leaf height, phytomass, forb and shrub cover increased, whereas utilization decreased (Table 4.2). Rain-induced floral changes included increases in phytomass, leaf height, grass and forb cover, and declines in utilization, litter and soil cover.

Significant biophysical differences exist among habitat types (Figures 4.1 and 4.2). Those variables which contribute most to discriminating habitat types, i.e. tree density, leaf height, utilization, herbaceous phytomass and forb cover, were highly correlated to topographic position (Table 4.3). This was confirmed by the primacy of topographic position as a canonical correlation coefficient. Expectedly, the man-created boma habitats were distinctive; characterized by low leaf height and litter cover, and high utilization and grass cover.

Floral char similar to those identified by discriminant analysis. The distribution of major habitat types (excluding bomas), proceeding downhill, was Treeless Grassland, *Balanites* Grassland, *Balanites-Acacia* Grassland and *Acacia* Woodland (Table 4.5).

4.3.2 Resource Use

Partitioning of resources was achieved by specialization in diet and habitat selection. These gradients, extracted by discriminant analysis, collectively identified unique resource use patterns for each ungulate species (Figures 4.3 and 4.4). On the basis of the primacy of the first discriminant functions from both topographic-floral and dietary data, secondary functions were removed, leaving two functions that could be meaningfully interpreted on a 2-dimensional territorial map. Table 4.6 lists the canonical correlations of environmental variables with each

Table 4.2. Effects of topography and season on environmental parameters (mean, standard error of the mean). Topographic differences evaluated by Student-Newman-Keuls procedure at p=0.05. U=Upper, M=Middle and L=Lower.

	Upper			Middle			Lower			Significance	
	Dry	Wet		Dry	Wet		Dry	Wet		Dry	Wet
Litter Cover (%)	9.2	3.4	<.05	10.4	4.1	<.05	11.2	4.6	<.05	NS	NS
	0.6	0.3		0.6	0.3		0.9	0.6			
Soil Cover (%)	14.9	7.2	<.05	15.7	8.4	<.05	16.6	6.1	<.05	NS	M≠U,L
	0.8	0.3		0.7	0.4		1.0	0.8			
Grass Cover (%)	75.8	88.9	<.05	73.6	86.5	<.05	69.9	87.8	<.05	L≠U,M	M≠U
	0.8	0.6		0.8	0.6		1.1	1.1			
Forb Cover (%)	0.0	0.4	<.05	0.1	0.6	<.05	0.5	1.1	<.05	L≠U,M	L≠U,M
	0.0	0.1		0.0	0.1		0.2	0.2			
Shrub Cover (%)	0.0	0.0	NS	0.3	0.4	NS	0.2	0.2	NS	NS	U≠M
	0.0	0.0		0.1	0.1		0.1	0.1			
Leaf Height (cm)	8.9	11.2	<.05	11.7	14.0	<.05	13.9	18.5	<.05	L≠M≠U	L≠M≠U
	0.4	0.5		0.5	0.4		0.8	0.8			
Utilization (%)	81.5	46.7	<.05	67.0	43.9	<.05	59.9	27.3	<.05	U≠M,L	L≠M,U
	1.9	1.4		2.4	1.8		3.9	3.5			
Tree (#/ha)	10.9	11.7	NS	50.4	41.1	NS	120.0	77.6	<.05	L≠M≠U	L≠M≠U
Density	1.6	1.4		5.5	3.8		9.0	8.4			
Phytomass	122.0	120.8	NS	142.6	150.6	NS	162.9	186.0	<.05	L≠M≠U	L≠M≠U
(g/m^2)	4.1	2.7		4.2	4.2		6.2	8.2			

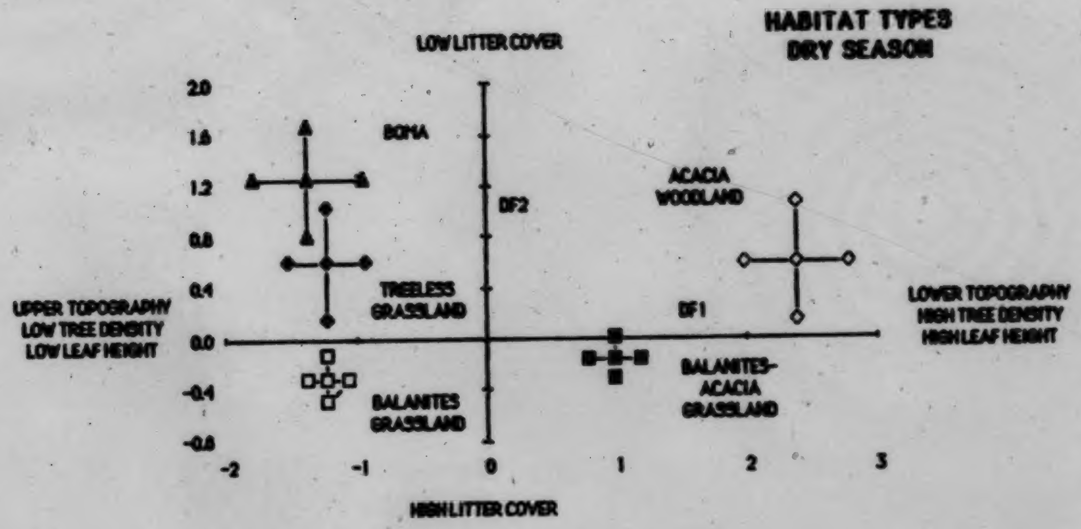

Figure 4.1 Ecological separation of habitat types during the dry season. Location of habitat centroids (+ / - 2 SE) according to the first two canonical variates.

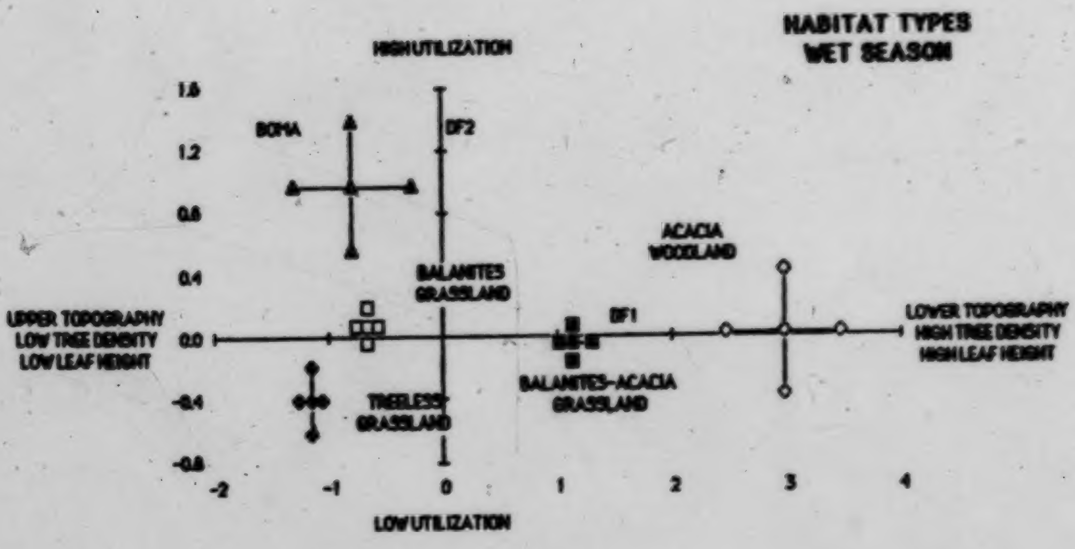

Figure 4.2 Ecological separation of habitat types during the wet season. Location of habitat centroids (+ / - 2 SE) according to the first two canonical variates.

Table 4.3. Pooled within-groups correlations between canonical discriminant functions and discriminating variables for habitat types.

	Dry Season		Wet Season	
	DF1	DF2	DF1	DF2
Ground Cover				
Litter Cover	0.10	-0.65	0.10	-0.12
Soil Cover	0.01	-0.12	0.04	-0.07
Grass Cover	-0.15	0.56	-0.12	0.14
Shrub Cover	-0.06	-0.24	0.07	-0.03
Forb Cover	0.12	0.00	0.15	-0.19
Topo-Floral				
Leaf Height	0.36	-0.35	0.34	-0.51
Phytomass	0.31	-0.24	0.31	-0.36
Utilization	-0.34	0.43	-0.23	0.81
Tree Density	0.56	-0.12	0.51	0.08
Topography	0.78	-0.03	0.87	0.00
Distance to Water	- 0.23	0.75	-0.26	-0.36
Canonical Correlation	78.9	40.9	75.4	26.6
Significance	<0.01	<0.01	<0.01	<0.01

Table 4.4. Biophysical description of habitat types.

	Treeless		Balanites		Balanites-Acacia		Acacia		Boma	
	Grassland		Grassland		Grassland		Woodland			
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Ground Cover (%)										
Litter Cover	5.7	2.9	10.8	3.7	11.3	4.5	10.0	4.9	4.6	2.0
Soil Cover	17.1	6.2	15.8	7.9	15.5	8.3	16.7	6.5	11.7	5.3
Grass Cover	77.2	90.5	73.0	87.8	72.4	86.3	70.3	86.7	83.7	92.7
Shrub Cover	0.0	0.0	0.4	0.2	0.2	0.3	0.1	0.1	0.0	0.0
Forb Cover	0.0	0.4	0.1	0.5	0.2	0.6	0.5	1.6	0.0	0.0
Topo-Floral										
Leaf Height (cm)	7.1	12.2	9.9	11.2	13.0	15.2	15.3	19.1	7.1	9.2
Phytomass (g/m^2)	107.4	127.3	128.2	124.0	154.3	160.5	173.5	186.9	110.5	107.5
Utilization (%)	86.7	42.0	77.0	49.6	61.0	35.6	54.2	26.6	96.6	69.2
Tree Density (#/ha)	5.2	1.8	15.4	15.7	86.6	53.5	118.9	89.0	7.8	13.6
Topography*	1.3	1.0	1.4	1.3	2.3	2.0	2.8	2.8	1.4	1.4

* 1-upper, 2-middle, 3-lower

Table 4.5. Association between habitat types and topographic position.

	Percent Observations	Topographic Level Upper	Middle	Lower
Habitat Types.				
Treeless Grassland				
Dry Season	8.6	17.1	6.1	0.0
Wet Season	15.3	27.7	1.7	0.0
Balanites Grassland				
Dry Season	34.3	63.1	28.2	1.4
Wet Season	43.7	57.7	35.4	0.0
Balanites-Acacia Gr.				
Dry Season	43.2	8.1	58.0	69.9
Wet Season	30.3	6.4	80.8	46.9
Acacia Woodland				
Dry Season	7.9	0.0	3.8	26.0
Wet Season	5.4	1.2	0.4	43.8
Fertile (Boma)				
Dry Season	6.0	11.7	3.8	2.7
Wet Season	5.3	7.0	12.5	9.1

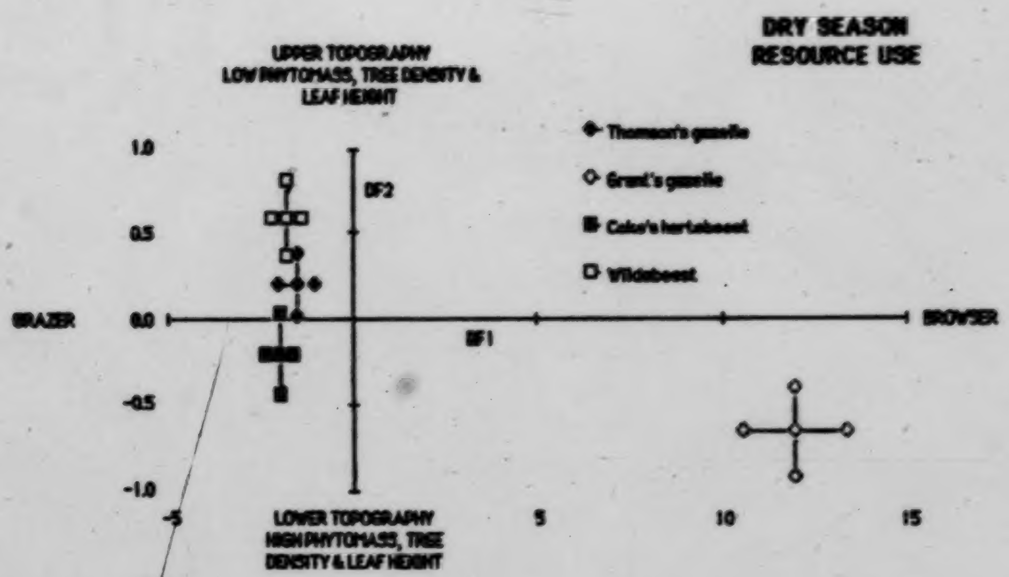

Figure 4.3 Resource division of ungulate species during the dry season. Location of species niche centroids (+/- 2 SE) according to the first canonical variate extracted from faecal analyses and topo-floral distribution.

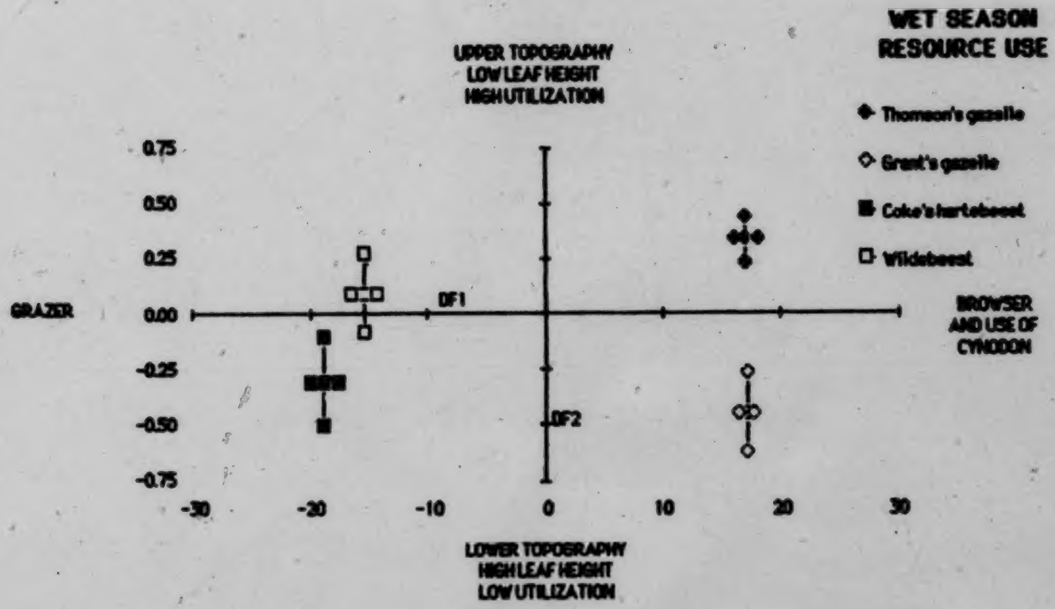

Figure 4.4 Resource division of ungulate species during the wet season. Location of species niche centroids (+/- 2 SE) according to the first canonical variate extracted from faecal analyses and topo-floral distribution.

discriminant function.

4.3.3 Diet

Ecological separation was apparent at the level of diet selection. Discriminant function 1 represents a gradient polarizing grass and dicotyledon forage. Grant's gazelle foraged extensively on dicotyledons, whereas hartebeest and wildebeest preferred grasses. Greater use of forbs and *Cynodon* by Thomson's gazelle generally maintained their distinctiveness from wildebeest and hartebeest.

Figures 4.3 and 4.4 suggest that dietary overlap decreased in the wet season. Although each species exhibited similar preferences for many forage species, gazelles preferred *Cynodon* and avoided *Pennisetum*. Wildebeest and hartebeest exhibited the opposite pattern in the wet season. High levels of browsing (both forbs and shrubs) maintained the distinctiveness of Grant's gazelle. As in the dry season, considerable dietary overlap existed between hartebeest and wildebeest.

4.3.4 Habitat

Striking differences exist in the environmental preference of ungulate species (Table 4.7). Discriminant function 2 reflects a plant community gradient closely related to topographic relief. Wildebeest and Thomson's gazelle occupied hilltops (Treeless Grassland and *Balanites* Grassland), Grant's gazelle topographic depressions (*Acacia* Woodland) and hartebeest intermediate areas (*Balanites-Acacia* Grassland; Table 4.8). Gazelle species and hartebeest exhibited an upward migration during the rainy season (Table 4.7), accounting for the greater amount of overlap along DF2. Distance to water contributed to discriminant function 2 in both seasons and indicated that Grant's gazelle and hartebeest were distributed furthest from water.

Table 4.6. Pooled within-groups correlations between canonical discriminant functions and discriminating variables for resource use.

	DIET (DF1)			BIOPHYSICAL (DF2)	
	Dry Season	Wet Season		Dry Season	Wet Season
Dicots			Ground Cover		
Aerva	0.26	0.07	Litter Cover	-0.11	-0.02
Grewia	0.35	0.02	Soil Cover	0.03	0.09
Hibiscus	0.19	0.02	Rock Cover	NS	NS
Pavonia	0.22	0.01	Grass Cover	0.12	0.01
Sida	0.12	0.00	Shrub Cover	-0.09	-0.11
Solanum	0.20	0.00	Forb Cover	-0.28	-0.35
Monocots			Topo-floral		
Chloris	-0.09	-0.01	Leaf Height	-0.57	-0.65
Cynodon	-0.09	0.05	Phytomass	-0.61	-0.40
Digitaria	-0.11	0.02	Utilization	0.52	0.59
Ischaeum	-0.08	-0.02	Tree Density	-0.61	-0.47
Lintonia	-0.05	0.00	Topography	-0.81	-0.63
Microchloa	-0.07	-0.07			
Pennisetum	-0.20	-0.10	Distance to		
Sporobolus	-0.05	-0.21	Water	-0.23	-0.26
Themeda	-0.20	-0.09			
Canonical Correlation	97.8	99.9		63.3	52.8
Significance	<0.01	<0.01		<0.01	<0.01

Table 4.7. Diet and resource use patterns during dry and wet seasons. Dietary differences evaluated by Student-Newman-Keuls procedure at p=0.05 level.[1]

	T. gazelle		G. gazelle		C. hartebeest		Wildebeest		Significance[2]	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
DIET										
DICOTS										
Aerva	0.4	0.3	30.2	16.0	0.0	0.0	0.0	1.4	A	A
Grewia	0.9	0.5	8.6	0.2	0.1	0.0	0.0	0.0	A	NS
Hibiscus	0.3	0.0	4.0	7.3	0.2	0.0	0.0	0.0	A	NS
Pavonia	1.6	0.7	17.0	0.0	0.0	0.0	0.6	0.0	A	NS
Sida	0.6	0.0	2.4	0.2	0.0	0.0	0.2	0.2	A	NS
Solanum	0.7	1.0	11.0	14.6	0.1	0.0	0.1	0.4	A	NS
MONOCOTS*										
Chloris	5.2	4.5	0.0	0.0	3.2	1.6	4.9	5.3	B	B
Cynodon	3.0	13.5	0.0	15.5	3.5	1.4	4.7	4.7	A	NS
Digitaria	7.0	7.5	0.1	5.7	10.2	5.1	11.7	2.4	A	NS
Ischaeum	0.9	3.3	0.0	2.9	8.2	6.2	3.2	4.2	C	NS
Lintonia	2.9	5.8	0.4	2.2	1.2	2.3	3.5	5.3	NS	NS
Microchloa	5.5	2.1	0.1	1.4	3.9	4.8	10.0	7.8	D	I
Pennisetum	11.7	0.0	0.0	0.0	14.9	13.4	12.9	9.7	A	G,H
Sporobolus	4.2	5.3	0.0	8.6	0.9	2.1	4.2	18.4	E	I
Themeda	38.2	40.8	2.5	10.6	34.6	48.4	25.2	25.1	A,F	E,J
BIOPHYSICAL										
Ground Cover										
Litter Cover	10.3	4.0	10.3	4.0	10.4	3.9	9.2	0.8	NS	NS
Soil Cover	16.7	7.7	14.9	7.5	15.5	7.1	14.2	7.4	NS	NS
Grass Cover	72.1	87.7	73.6	87.4	73.6	88.0	76.6	89.1	NS	NS
Shrub Cover	0.3	0.2	0.2	0.4	0.3	0.1	0.0	0.1	NS	NS
Forb Cover	0.2	0.4	0.3	0.7	0.1	0.7	0.0	0.7	NS	K
Topo-Floral Characteristics										
Leaf Height	10.2	11.6	13.0	14.4	12.5	14.3	9.7	12.7	D,K	K
Phytomass	129.6	130.3	159.4	143.7	147.7	151.7	126.8	133.9	D,K	M
Utilization	75.4	49.3	62.4	36.6	64.2	38.9	76.6	45.3	B,L	K
Tree Density	47.3	22.1	81.9	35.1	58.0	41.6	28.9	21.7	A,D	K,L
Topography	1.8	1.5	2.3	1.8	1.9	1.7	1.5	1.5	B,L	B,L
Distance to Water	1697	1293	1958	1445	1872	1537	1652	1374	NS	NS

[1] Values (arcsin transformed) expressed as percent of total dietary observations.

[2] T=Thomson's gazelle, G=Grant's gazelle, C=Coke's hartebeest, W=Wildebeest

(NS) NOT SIG.	(A) G=T,C,W	(B) G=W,T	(C) C=G,W,T	(D) W=C,G	(E) W=C
(F) W=C,T	(G) T=W,C	(H) G=W,C	(I) W=T,C,G	(J) G=T,C	(K) T=C,
(L) C=W,T	(M) T=C				

Table 4.8. Association between habitat types and ungulate distribution.

	Percent Observations	Thomson's gazelle	Grant's gazelle	Coke's hartebeest	Wildebeest
Habitat Types.					
Treeless Grassland					
Dry Season	8.6	12.1	3.2	5.3	11.3
Wet Season	15.3	17.2	11.6	11.0	21.8
Balanites Grassland					
Dry Season	34.3	40.3	14.3	28.0	52.8
Wet Season	43.7	50.5	32.6	39.0	46.0
Balanites-Acacia Gr.					
Dry Season	43.2	34.7	50.8	58.7	32.1
Wet Season	30.3	22.8	39.9	37.5	28.7
Acacia Woodland					
Dry Season	7.9	5.6	19.0	5.3	1.9
Wet Season	5.4	2.8	10.1	8.1	2.3
Fertile (Boma)					
Dry Season	6.0	6.5	12.7	2.7	1.9
Wet Season	5.3	6.3	5.8	3.7	1.1

4.4 Discussion

4.4.1 Environmental Matrix

The catena is a prevailing feature of African grasslands where topographic relief occurs (Anderson and Talbot, 1965; Anderson and Herlocker, 1973). Although vertical relief at the study area seldom exceeds 50 m, it was sufficient to influence the distribution of soil types (Reed, 1983) and establish a gradient in soil moisture (Stelfox, unpubl.). Proceeding downhill, the catena was characterized by an increase in leaf height, herbaceous phytomass, tree density and forb and shrub cover, and a decline in grass utilization.

Habitat types, identified by density and presence of tree species, were highly correlated to topographic position. Since habitat overlap on the topographic gradient was minimal, this classification scheme offers a quick and simple, though meaningful, way of characterizing the biophysical resources of native ungulates.

4.4.2 Diet Selection

Forage selection accounted for a considerable level of ecological separation among the ungulate species. The results largely confirm that wildebeest and hartebeest are grazers preferring bulk and roughage, while Thomson's and Grant's gazelle are intermediate feeders foraging on both grasses and browse (Hofmann, 1973). The amount of browse in the diet of Grant's gazelle significantly exceeded that of Thomson's gazelle. Other studies indicating that hartebeest and wildebeest forage exclusively, or predominantly, on grasses include Lamprey (1963), Casebeer and Koss (1970), Stewart and Stewart (1970) and Owaga (1975). Preference for dicotyledons by Grant's gazelle has been reported by Talbot and Talbot (1962), Stewart and Stewart (1970), and Spinage, Ryan and Shedd (1980).

In the wet season, when all species relied extensively on grasses, gazelles remained distinct from the bulk grazers, i.e. hartebeest and wildebeest, by selecting *Cynodon* and avoiding *Pennisetum*. Distribution of *Cynodon*, recognized as a preferred forage species in East Africa

(Pratt and Gwynne, 1977), was largely restricted to boma habitats where inputs of nitrogen and intense utilization and trampling provide a competitive advantage to this prostrate perennial (Chapter 6). Studies of these fertile sites indicated that gazelle use was significantly higher at bomas than in surrounding rangeland (Table 6.6). Small patches of *Cynodon*, confined to the proximity of bomas, may be less suitable for the grazing movements of the larger herds of hartebeest and wildebeest. As cattle populations on WRR are reduced to encourage wildlife, the eventual loss of "fertile" areas may remove a unique habitat providing ecological separation of gazelles and alcelaphines (hartebeest and wildebeest).

Consistent with the findings of this study, intake of browse has been reported to increase in the dry season for Thomson's gazelle (Bell, 1970) and Grant's gazelle (Stewart and Stewart, 1970). The relative amount of grass and browse in gazelle diets is determined primarily by forage phenology. Grasses are most desirable during early growth stages before tissues lignify and protein levels and digestibility decline (Van Soest, 1982). High concentrations of digestibility-reducing agents such as condensed tannins are thought to discourage use of browse when nutritious grasses are available (Reed, 1983). In the dry season, browse is comparatively high in protein and digestibility, providing better forage than mature grasses consisting primarily of fibrous supportive tissue (Jarman and Sinclair, 1979). Significant declines in the dry season nutritional value of grasses, as evaluated by protein and acid detergent fiber, occurred in the study area (Chapter 7; Reed, 1983). Growth flushes of woody vegetation in late dry season provide high protein forage during a time of critical need (Rushworth, 1975).

Most forbs located in upper topographic areas were ephemeral, existing for only a short time early in the rainy season. Presence of these species in wet season faeces may not indicate selectivity, but rather use proportional to availability. This would explain the higher percent of dicots in the wet season diet of wildebeest.

Dietary overlap, at the plant species level, is not convincing proof of competition for food. Gwynne and Bell (1968) have documented partitioning of ungulate forages at the level of plant part (i.e. sheath, leaf and stem) for wildebeest, zebra (*Equus burchelli*) and topi (*Damaliscus korrigum*). Facial conformation influences ungulate foraging strategies by affecting access to and procurement of herbage (Leuthold, 1977; Kingdon, 1982). In general, smaller ungulates possess narrow mouths that are adapted for selecting small, though nutritious, plant parts. Contrastingly, large herbivores are equipped with dentition enabling rapid ingestion of undifferentiated forage of low quality. This morphological trend may also occur within small size ranges. For example, the wide flat muzzle of wildebeest is suited to homogenous swards of low growing grasses, whereas the relatively narrow mouth of the smaller hartebeest is adapted to selecting individual leaves from tall grass tillers.

Since first popularized by Vesey-Fitzgerald (1960), numerous studies have shown that the foraging patterns of one species may improve the plant community for subsequent herbivores. Thomson's gazelle in the Serengeti ecosystem prefer areas previously supporting wildebeest, whose grazing creates a short grass sward exposing nutritious herbs and encouraging active regrowth of prostrate leafy grasses (Jarman and Sinclair, 1979). This example of resource facilitation might explain the close topographic association recorded by these two species in this study.

4.4.3 Distributions along the Catena

Topography, by affecting ungulate mobility, forage quality and heat balance, appears to determine patterns of resource use within the ungulate community. By residing in the valley bottoms, Grant's gazelle improve their access to the browse species which dominate their diet. Hartebeest prefer lower hillsides which are dominated by tall grasses. Upper areas, characterized by heavily-utilized and low growing herbaceous vegetation, are suited to the foraging preferences of wildebeest and Thomson's gazelle. Interestingly, those species with most similar food preferences at the species level, i.e. Thomson's and Grant's gazelle, and hartebeest and wildebeest, were most dissimilar in topographic distribution. The greatest amount of topographic-dietary overlap existed between Thomson's gazelle and wildebeest.

With the onset of the rainy season, ungulates exhibited an uphill migration, increasing the degree of species overlap along the topographic gradient. Ungulates appeared to avoid lower topographic levels in the wet season because of poor footing caused by swollen clay soils. Reduced mobility may in turn predispose animals to predation. In support of this hypothesis, flight distances of animals observed in valley bottoms during the rainy season were noticeably higher (Stelfox; unpubl.). High sand content of eluvial upper level soils would not encumber movement. Studies by Talbot and Talbot (1963) and Anderson and Herlocker (1973) have also documented that large herbivores avoid heavy textured soils during the rainy season.

As the moisture deficit intensified in the dry season, animals were observed to move down the catenary sequence. Undoubtedly, this movement can be interpreted as an effort to relocate in areas where grasses have not been depleted and where dicotyledenous plants are more common. I believe that animals were also seeking trees, particularily *Balanites*, for shade from intense sunlight. Shading behaviour was commonly observed between 1200 and 1700 h during the hotter months (January/February/March) for all species except Grant's gazelle.

Related to heat tolerance, Grant's gazelle were located furthest from available surface water. This species is xeric in distribution (Kingdon, 1982), and capable of fulfilling its water requirements from succulent forages and hygroscopic plants (Taylor, 1968). The concentrated urine of Grant's gazelle also prevents excessive water loss (Hofmann, 1973).

4.4.4 Implications for Management

Problematic range conditions at WRR include the accumulation of senescent phytomass in valley bottoms and overutilization of hilltops. These related features reflect an uneven distribution of herbivores. Factors contributing to this imbalance include the earlier floral green-up occuring along hilltops and ridges (Table 7.2) and impaired mobility caused by swollen clay soils in the depressions. Once a gradient in phytomass has been established by uneven foraging pressure, excessive litter perpetuates the problem. Given time constraints, it is reasonable that herbivores would avoid areas where palatable forage can only be obtained by sorting through a physical barrier of vegetative litter. Not until the dry season, when hilltops and upper slopes have been denuded of herbaceous vegetation, does the collective ungulate community forage extensively in lowlands. Declines in body condition late in the dry season, as recorded for Thomson's and Grant's grazelle (Chapter 7), emphasize the reduction in forage quality and the necessity for altering foraging strategies. Lower topographic grasses such as *Ischaeum, Pennisetum* and *Lintonia* prosper under conditions of relaxed herbivory and are of poor nutritional value (Reed, 1983). A higher level of defoliation can stimulate primary productivity and increase forage quality by maintaining a high shoot/root level, hormonal redistribution, improved light penetration and nutrient recycling (McNaughton, 1979). His studies in the Serengeti indicate that moderate levels of defoliation are required to maintain forage quality (i.e. leaf/stem ratio), species diversity and the presence of prostrate grazophils. It follows, therefore, that a primary goal of WRR management is to encourage more even foraging pressure.

Research on prescribed burning (Chapter 5) demonstrated that fire can effectively suppress topographic-floral gradients such as dead phytomass and encourage a more even distribution of native ungulates. By opening up more available habitat, burning could increase population levels while providing needed dry season forage. Since fire increases mortality of shrubs and trees (Buechner and Dawkins, 1961; Phillips, 1965; Langlands, 1967; Scott, 1971), a regular burning program may be deleterious to browsers such as Grant's gazelle and giraffe (*Giraffa camelopardalis*). By reducing environmental variability, fire may actually increase inter-specific overlap in resource use.

An alternative strategy for removing fibrous grasses is to increase zebra populations. Equids, by nature of their monogastric digestive system, may require more forage than ruminants of equal weight (Foose, 1982). To compensate for increased intake demands, zebra forage unselectively, often on rank grasses (Kingdon, 1982). Comparisons of foraging strategies indicated that zebra digesta contained lower levels of protein and higher amounts of fiber than several ruminant species (Hoppe, 1977). In the Serengeti ecosystem, zebra are the first species to move down the catena and utilize coarse forage (Bell, 1970). By reducing leaf height and encouraging regrowth, their foraging activities encourage downward migrations of wildebeest and Thomson's gazelle.

4.5 Summary

Distinctive resource use patterns of Thomson's gazelle, Grant's gazelle, hartebeest and wildebeest were identified. This is not to imply, however, that ecological overlap was absent. Each species exhibited preferences for a unique set of biophysical resources, while displaying considerable flexibility in occupational patterns as they responded to changing environmental conditions. As emphasized by Walker (1979), it is the adaptability of native ungulates which encourages even use of a broad spectrum of resources in space and time. Environmental parameters important in segregating species included a topographic-floral gradient and the relative amount of dietary grass and browse. Avoidance of wet clay soils may have resulted in elevational compression of the ungulate community in upper levels during rainy seasons. High forage quality and minimal dietary overlap during this season ensured good body condition and prevented intense competition. With the exception of Thomson's gazelle and wildebeest, inter-species resource overlap was minimized in that those species exhibiting similar dietary preferences were most widely separated along the topographic gradient.

A proposed habitat classification scheme was shown to be biophysically meaningful. Those environmental gradients discriminating habitat types, i.e. topographic position, tree density, leaf height and utilization, etc., were similar to ones maintaining ecological separation of ungulate species. It would appear that resource managers can therefore evaluate resource availability for each ungulate species by monitoring habitat types.

Accumulations of undigestible plant litter is thought to discourage ungulate use in valley bottoms. Prescribed burning programs and a larger zebra population are two managerial options that could reduce litter phytomass and encourage more balanced use of resources. Although promoting higher biomass densities of wildlife, a more homogenous environment would likely increase inter-specific competition and encourage a less diverse ungulate community.

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Chapter 5

Effects of Fire and Topography on the Athi Plains Ecosystem, Kenya

5.1 Introduction

Fire is an historic force that has shaped and maintained African grasslands (West, 1965; Scott, 1970). Its magnitude is indicated by the prevalence of fire-adapted plants and the drastic changes in vegetation which often accompany fire suppression (Heady, 1960). This has lead to the belief that much of Africa's grasslands are in a fire-deflected subclimax state (Glover, 1968). Despite numerous studies, effects of fire on grassland ecosystems remain controversial (Thomas and Pratt, 1967). Much of this uncertainty reflects regional or local differences in meteorology, flora and fauna (Lemon, 1968); yet some can be attributed to inadequate quantification of the fire and to the use of different criteria for evaluation (Daubenmire, 1968).

All too often, the effects of range fires are related to the fire event itself and not to the relevant processes (Trollope, 1981). To gain a deeper understanding, it is important not to view fire as an independent agent, but rather as a factor which affects and is affected by other components of the ecosystem. Recent contributions to this approach are provided by Norton-Griffiths (1979) and Pellew (1983).

On the landholdings of Wildlife Ranching and Research Ltd., topographic gradients in plant community structure are thought responsible for unbalanced resource use by ungulates (Chapter 4). Vegetation features in topographic depressions which discouraged grazers included accumulations of grass litter, grasses of advanced phenological stage and high tree density. Two experimental prescribed fires were conducted to quantify the effects of fire on grassland community structure, forage production, quality and utilization, tree mortality and ungulate distribution. The effects of topography on local flora and fire behaviour were also documented.

5.2 Methods

Two experimental prescribed fires were conducted. Fire A was used to elucidate interrelationships between fire, plant community structure and animal distribution. Fire B was planned to demonstrate the use of fire as a management tool for inducing tree mortality, reducing litter accumulation and broadening animal distributions. The following methodologies pertain to Fire A, except for the last section on ungulate distributions which refer to Fire B.

5.2.1 Fire Description

The prescribed fire at Site A (17.5 ha in size) was conducted between 1200 and 1400 h on 21 September 1982, approximately three weeks prior to the onset of the rainy season. At this time grass was completely cured. The literature suggests that late dry-season fires are preferred in Africa (West, 1965; Van Rensburg, 1972; Edroma, 1984). By exposing the soil surface to wind and sun for extended periods, fires conducted earlier in the dry season can lead to excessive soil erosion and desiccation (Cook, 1965), whereas waiting until photosynthetic activity has begun can depress post-fire productivity and increase grass mortality. Both burn and contiguous control sites were 250 X 700 m with their length oriented from the top to the bottom of a topographic gradient. Air temperature, relative humidity, wind speed, and cloud cover were recorded during the burn. Wind speed was measured with an instantaneous hand-held anemometer located upwind of the fire at a height of 1.2 m above ground. Wind direction was determined by orienting the anemometer until maximal readings were recorded. Air temperature and relative humidity were monitored by a hygrothermograph located four km from the fire. Cloud cover was estimated visually. Ignition began along the lower edge of the fire area and progressed upslope in the direction of the prevailing wind. Head fire ignition was chosen in accordance with Trollope's (1978) findings that backfires depress grass recovery and productivity. The fire area was delineated into three equal segments (upper, middle and lower) and the time required for each third to burn was recorded. Areas where wind and/or fuel were insufficient to sustain fire spread were reignited.

Three random 0.5x0.5 m plots were clipped of standing crop and litter immediately before and after the fire for each of the three topographic levels on the site to determine the amount of material combusted. These samples were air-dried to a constant weight (a drying oven was not available) then corrected for residual moisture to estimate oven-dry weight using the equation given by Noble, Bary and Gill (1980) for grass fuels:

$$M = (97.7 + 4.06*H)/(T + 6.0) - (0.00854*H) + 3000/C - 30.0$$

where M=fuel moisture content (%), H=relative humidity (%), T=air temperature (°C) and C=degree of curing (%) The appropriate values at the time of weighing, following air-drying, were T=28°C, H=42%, and C=100%, yielding a fuel moisture content of 7.75 percent.

Frontal fire intensity for each topographic level was determined according to Byram's (1959) formula (after Alexander, 1982):

$$I = H*w*r/60$$

where I is frontal fire intensity (kW/m), H=low heat of combustion, w=weight of fuel consumed (kg/m^2), and r=rate of spread (m/min).

5.2.2 Plant Community Structure

For both burn and control sites, 3 random 0.5x0.5 m samples were clipped monthly at each topographic level to monitor phytomass and air-dry moisture content. In August 1983, three randomly located 0.5x0.5 m samples were collected from each of the six sub-sites to measure unattached litter phytomass.

Three 1x1x1 m randomly located exclosures were established in the control area at each topographic level to monitor primary productivity. The same was done for the burn area, except that two replicates were used. At the onset of the study each exclosure was clipped to a 2 cm height and all phytomass was removed. One year after the fire treatment, the phytomass in the exclosures was reclipped to determine primary productivity. These samples were analyzed by Norwest Feed Research Ltd, Edmonton, Alberta, Canada, for protein, fiber, lignin, ash, calcium and phosphorus. Neutral detergent fiber, fiber and protein were determined according to methods outlined by Horowitz (1980).

Step-point transects were conducted between September 1982 and March 1983 and in June and July 1983 to quantify the floristic composition and physical structure of the plant community in both sites at each of the three topographic sections. A thin incremented pin was lowered to the ground at each of 25 steps along eight transects originating at a central stake and bearing on ordinal and subordinal directions, yielding a total of 200 points per sampling site. At each point data were collected on species composition, utilization and leaf height. This technique is a form of point quadrat sampling and is described by Evans and Love (1957) and evaluated by Walker (1970), Mueller-Dombois and Ellenberg (1974) and Mentis (1981). To avoid observer bias, each transect was traversed using a compass bearing while not looking at the ground when proceeding from one point to the next.

Ocular etimates of herbaceous cover, phytomass, utilization and leaf height were conducted prior to step-point transects. Rangeland within 25 m of the central stake was evaluated by traversing the area for 10 minutes on foot. These calibrated estimates enabled quick and accurate characterization of the plant community for ungulate resource use (Chapter 4) and body condition studies (Chapter 7). Appendix 5.1 indicates the accuracy of ocular estimates as compared to objective step-point transects.

Fire-induced tree mortality was estimated in August 1983. Eight circular plots with diameters of 50 m were placed at 100 m intervals across the topographic gradient of both burn and control sites. Within each plot, all trees were categorized according to the portion of their crown which was dead.

5.2.3 Ungulate Distributions - Fire A

Counts were conducted frequently (>20/month) to quantify the number and topographic location of native ungulate species on the control and burn site. Using a motorcycle, it was possible to traverse the firebreak separating the burn and control sites and count animals before they moved appreciably.

5.2.4 Ungulate Distributions - Fire B

The second fire was conducted between 1100 and 1700 h on 30 and 31 March 1983 to determine the effects of a large burned area (1120 ha) on animal distributions. As perceived by Ranch management, undesirable features of the vegetation in this area included high densities of the tree *Acacia drepanolobium* and excessive accumulations of litter. The fire was conducted late in the dry season to encourage a high percentage of tree mortality. Norton-Griffiths (1979) has shown that late dry season fires are more damaging to trees than ones conducted earlier.

Ignition occurred along the eastern border of the area and proceeded as a head fire under the influence of a westerly wind. Fire spread was frequently inhibited in the sparse vegetation along hilltops, necessitating re-ignition. An existing road network provided a firebreak along the western, southern and eastern bounderies of the fire area.This 7.15 km road section served as a survey route to study ungulate distribution. All animals within 200 m of the road on the burned and unburned sides were counted. Surveys were conducted twice monthly for four months prior to and then repeated bimonthly during the four months following the fire.

5.3 Results

All data described below were collected from Fire A with the exception of supplemental information concerning ungulate distribution.

5.3.1 Weather and Fire Characteristics

During the burning period, air temperature increased gradually, relative humidity decreased, and cloud cover and wind speed/direction fluctuated slightly (Table 5.1). Reflecting top to bottom trends of increasing phytomass and fuel consumption, rate of spread and fire intensity increased with a drop in topographic position (Tables 5.2 and 5.3). Trends in fire characteristics across topography were probably ameliorated since temperature increased and

Table 5.1. Weather observations recorded during Fire A.

Time (h)	Air temperature (°C)	Relative humidity (%)	Cloud cover (%)	Wind speed (km/h)	Wind direction
1200	24	54	45	0	-
1230	24	52	45	5	S
1300	25	50	50	7	SW
1330	27	46	60	8	S
1400	28	42	55	5	SE
mean	26	49	51	5	S

Table 5.2. Physical fuel characteristics and fire impact on rangeland fuels for the three topographic levels of Fire A.

Position on slope	Fuel moisture content * (%)	Preburn fuel load(kg/m^2)	Postburn fuel (kg/m^2)	Fuel reduction (%)
Upper	9.9	0.186 (.055)**	0.081 (.013)	56.5
Middle	8.7	0.361 (.068)	0.111 (.004)	69.3
Lower	7.8	0.295 (.023)	0.083 (.025)	72.0

* Estimate based on Noble et al. (1980).

** Standard error of the mean.

Table 5.3. Component variables and calculated frontal fire intensities for the three topographic levels of Fire A.

Position on slope	Heat of combustion* (kJ/kg)	Fuel consumed (kg/m^2)	Rate of spread (m/min)	Frontal fire intensity (kW/m)
Upper	18,462	0.105	3.84	124
Middle	18,491	0.250	6.12	472
Lower	18,513	0.212	10.8	706

*Represents standard low heat of combustion of 18,700 kJ/kg reduced 24 kJ/kg per moisture content percentage point (Alexander, 1982).

relative humidity decreased as the active flame front proceeded uphill. It was estimated that between 85 and 90 percent of the Fire A site was burned over.

5.3.2 Plant Community Structure

On the control site, phytomass increased and plant moisture content decreased down the catenary sequence (Figs. 5.1 and 5.2). On the burn site, topographic trends in these parameters were not apparent. Relative to the control, phytomass was lower and moisture content was higher on the burn, although the difference became less pronounced as the study progressed. As determined by step-point transects, leaf height increased and utilization decreased for both sites with a drop in topography (Figs. 5.3 and 5.4). The disparity was much less on the burn.

Litter phytomass was approximately four times as high on the control site and increased significantly with a drop in topography (Table 5.4). Litter was uniformly low throughout the burn site. Primary productivity was not influenced significantly by the burn treatment or topography (Table 5.4). The low number of exclosures used in this study may have contributed to this observation.

5.3.3 Plant Nutrient Quality

The nutrient content of current year's growth did not differ greatly with treatment or topography (Table 5.5). Of the seven parameters tested, the only significant differences were higher protein in the control site and higher phosphorus and protein in the upper topographic levels. Treatment and topographic effects were not apparent for neutral detergent fiber, lignin, ash and calcium.

5.3.4 Plant Species Composition

The effects of fire on species composition were based on the last series of transects completed in July 1983. On the control, the low growing species *Themeda* and *Digitaria* decreased down the catena, whereas the tall and stemmy *Pennisetum* and *Ischaeum* increased.

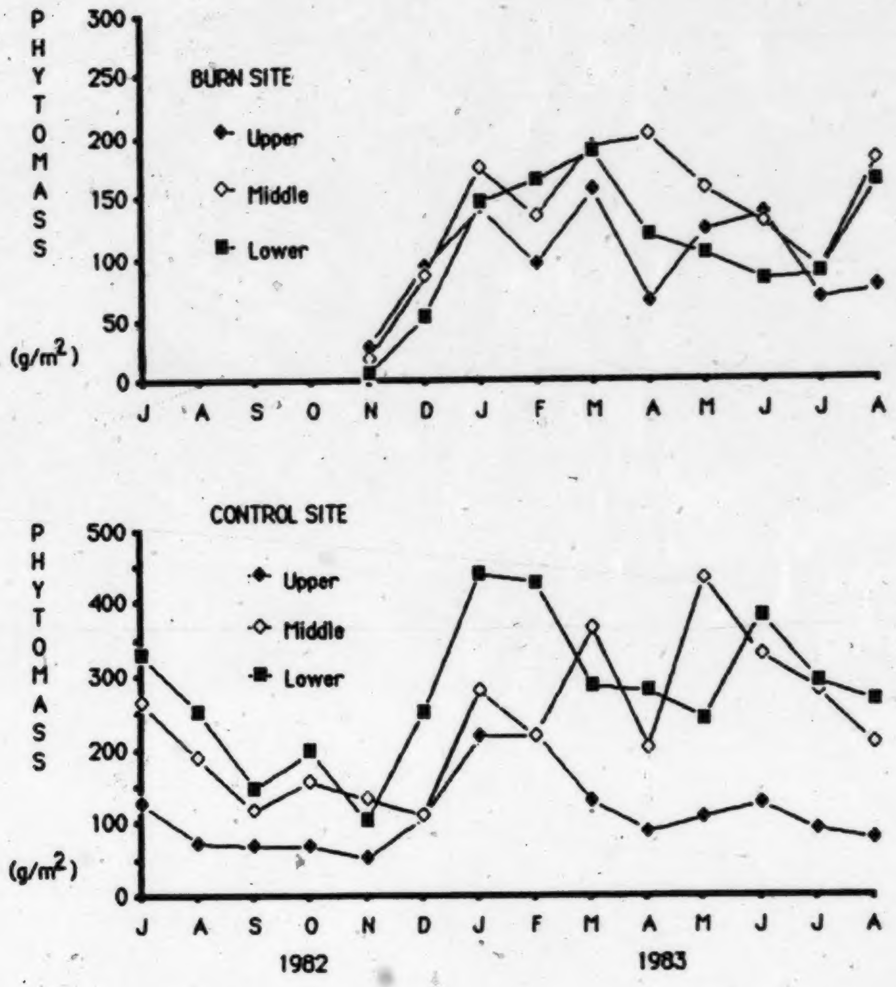


Figure 5.1 Effects of fire and topography on plant phytomass. Phytomass refers to all plant material present at conclusion of study.

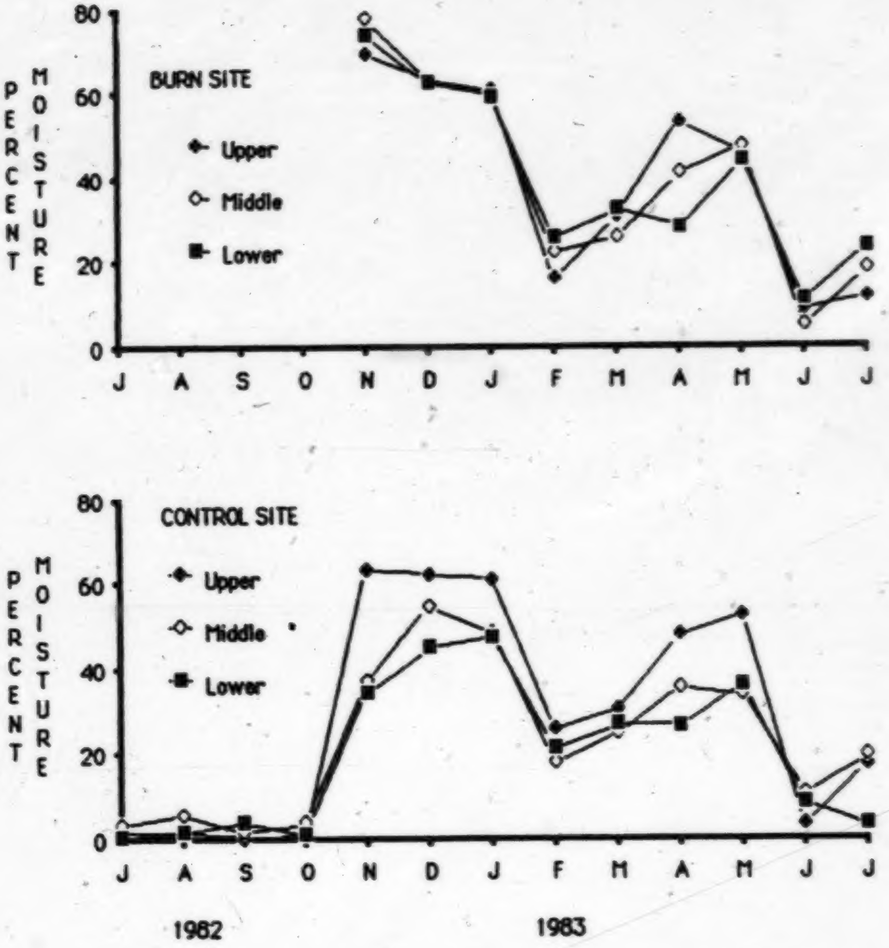


Figure 5.2 Effects of fire and topography on plant moisture content.

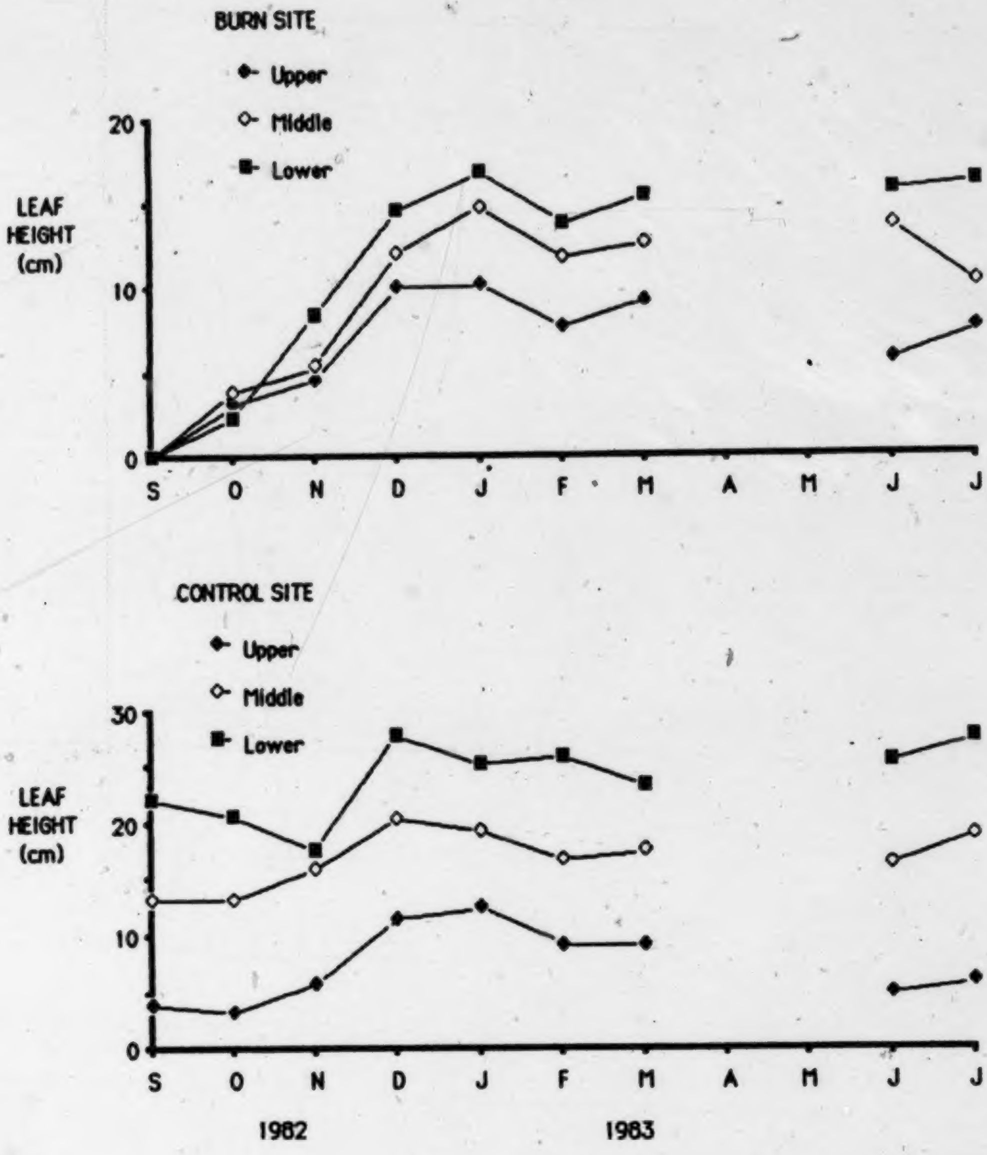


Figure 5.3 Effect of fire and topography on leaf height.

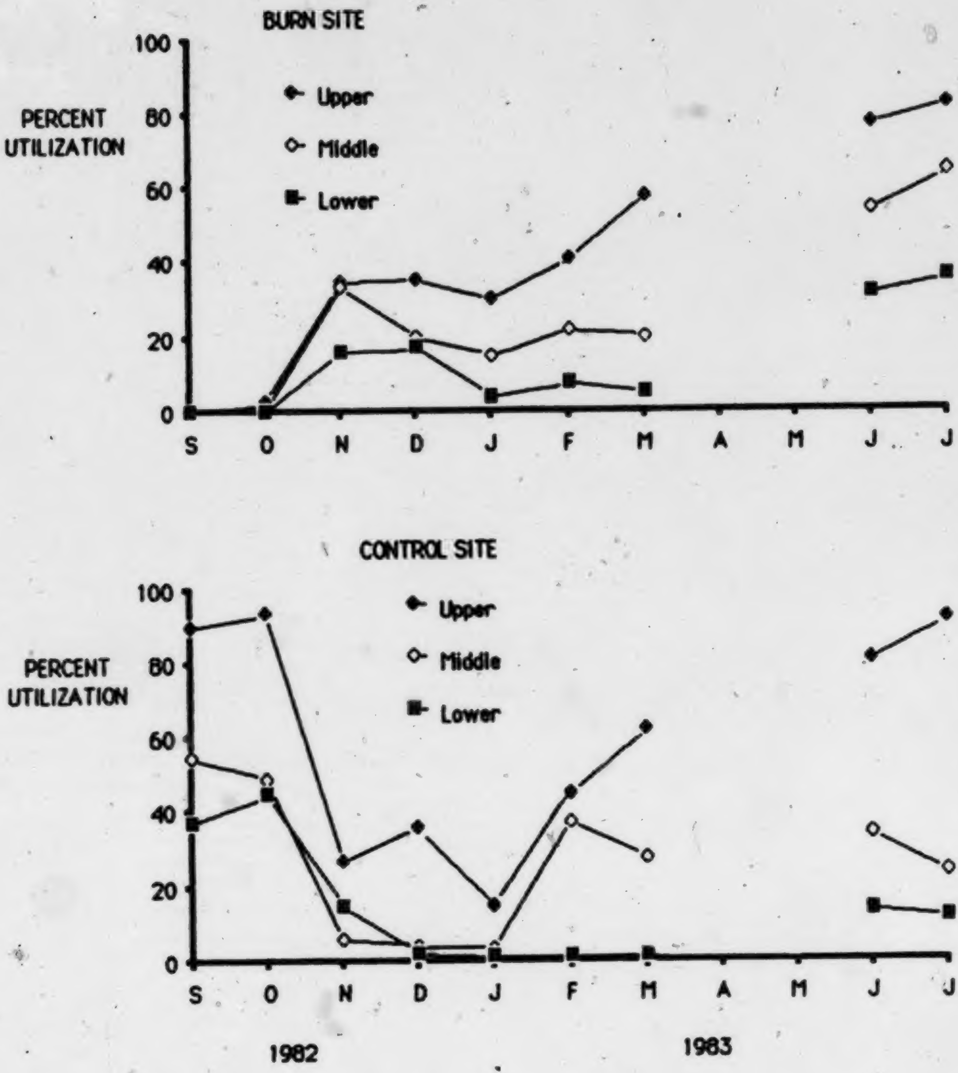


Figure 5.4 Effect of fire and topography on grass utilization.

Table 5.4. Effects of fire and topography on litter phytomass and primary productivity.

	Litter (g/m^2)			Productivity ($g/m^2/yr$)		
	N	X	se	N	X	se
Burn						
Upper	3	24.0	2.3	2	437.6	122.8
Middle	3	31.0	3.8	2	551.4	3.0
Lower	3	32.0	5.0	2	313.6	28.0
Total	9	29.0	2.6	6	434.2	54.3
Control						
Upper	3	56.0	10.0	3	594.5	31.2
Middle	3	138.7	26.7	3	419.5	77.0
Lower	3	150.7	20.1	3	355.3	87.1
TOTAL	9	115.1	18.9	9	456.4	49.8
Anova						
Treatment	1	<0.01		1	NS	
Topography	2	<0.01		1	NS	
Interaction	2	<0.05		2	NS	

Table 5.5. Effects of fire and topography on plant nutrients.

		Protein (%)		NDF (%)		Lignin (%)		Fiber (%)		Ash (%)		Calcium (%)		Phosphorus (%)	
	N	X	se	X	se	X	se	X	se	X	se	X	se	X	se
Burn															
Upper	2	4.5	0.2	73.9	2.0	7.7	0.4	52.2	1.5	11.8	1.0	.45	.04	.16	.01
Middle	2	3.6	0.1	72.8	1.2	7.5	0.1	54.1	1.4	12.4	1.6	.35	.16	.06	.01
Lower	2	3.7	0.2	73.3	1.8	7.3	0.9	54.1	0.7	12.3	0.5	.35	.06	.10	.02
Total	6	3.9	0.2	73.3	0.8	7.5	0.3	53.4	1.1	12.4	0.5	.39	.03	.11	.02
Control															
Upper	3	5.8	0.2	70.9	0.3	6.4	0.3	47.8	0.1	11.0	0.3	.42	.03	.18	.01
Middle	3	3.6	0.2	70.4	1.0	8.3	0.4	51.2	2.5	13.2	0.4	.38	.02	.09	.01
Lower	3	4.4	0.2	72.2	1.1	7.6	0.3	53.8	0.5	13.3	1.4	.52	.06	.12	.01
Total	9	4.6	0.3	71.2	0.5	7.4	0.3	50.9	1.1	12.4	0.5	.44	.03	.13	.01
Anova															
Treatment		<0.01		NS		NS		NS		NS		NS		NS	
Topography		<0.01		NS		NS		NS		NS		NS		<0.01	
Interaction		<0.05		NS		NS		NS		NS		NS		NS	

Although major changes in species composition were not indicated, it appeared that the topographic disparity was less pronounced on the burn site.

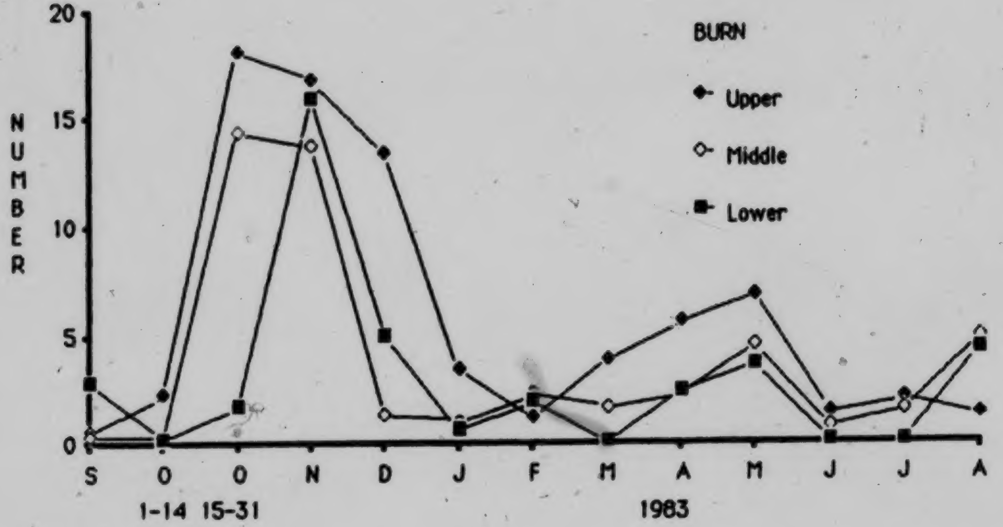
5.3.5 Tree Mortality

Relative to the control site, above-ground tree mortality was higher in the burn; ***Acacia drepanolobium***, 43.3% (Burn), 6.6% (Control); ***Balanites glabra***, 16.7% (Burn), 5.8% (Control). It is assumed that the difference in tree mortality can be attributed to the fire treatment. On the burn, mortality intensified with a drop in topography. Whereas 31.4% of the control trees showed no evidence of damage, only 4.9% of the burned trees were in a similar state. Of those *Acacia* whose aerial phytomass had been totally killed by the fire, over 82% exhibited some coppice regeneration near the base of the tree. This regrowth seldom occurred for trees which partially or totally survived the fire. Accumulations of dried grass beneath *Acacia*, the result of grazers avoiding the long thorns of this low growing tree, resulted in localized flare-ups that allowed the fire to penetrate the tree crown.

5.3.6 Ungulate Distribution

During the 3 week period following Fire A and prior to the onset of the mid-October rains, ungulate density was marginally higher on the control site. Immediately following the rain-induced green-up, wildlife were significantly more numerous on the burn (Fig. 5.5). Coinciding with the rainy seasons of October-December and February-April were substantial increases in the numbers of gazelles counted on the burn site. In decreasing abundance, the species were Thomson's gazelle, Coke's hartebeest, Grant's gazelle and wildebeest. With the exception of wildebeest, which appeared to avoid both treatment and control sites, this trend reflected the Ranch's population level of each species.

On the control site, ungulates preferred upper levels during the wet months, while shifting to lower areas during the dry season (Fig. 5.5). Monthly ungulate surveys between 1981 and 1983 for the entire Ranch revealed similar topographic migrations (Chapter 4).



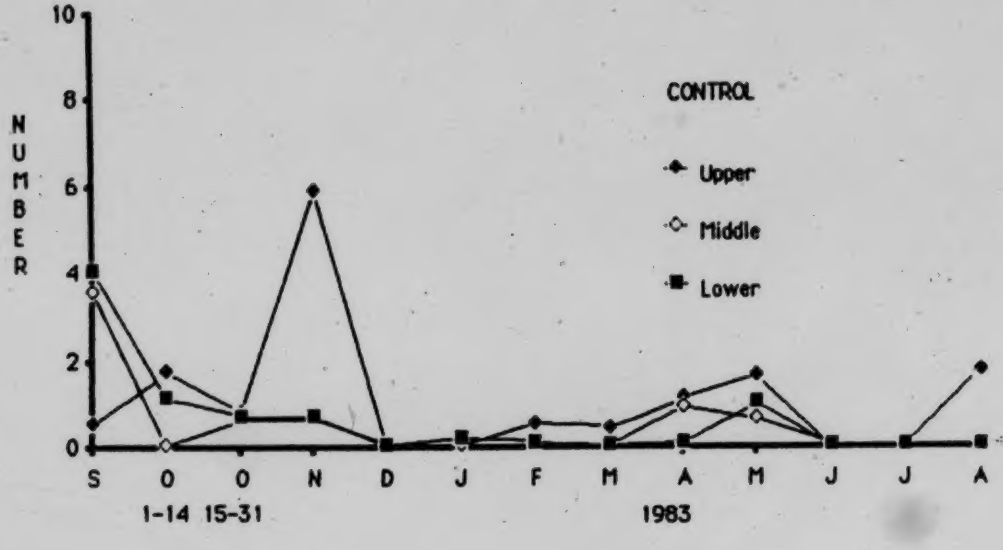


Figure 5.5 Effects of fire and topography on distribution of native ungulates (values represent number of animals observed on each topolevel).

Contrastingly, animals were more evenly distributed across the topographic gradient on the burn site.

At Site B prior to the burn, ungulate numbers were similar on the burn and control survey strip. During the four months following the treatment, ungulate density was significantly higher ($p<0.01$) on the burn strip (Table 5.6).

5.4 Discussion

Topography exerts a marked influence on vegetation. Proceeding downhill, increases in tree density, leaf height, litter and phytomass, and declines in utilization were conspicuous. These results are in agreement with other studies at WRR (Chapter 4; Reed, 1983). In that precipitation is considered the primary determinant of plant community structure and productivity in semi-arid Africa (Pratt and Gwynne, 1977; Tinley, 1982), these topographic-floral trends could be viewed as responses to soil moisture. Other factors being equal, increased availability and longer residency of soil moisture should enhance primary productivity in lower areas (Jarman and Sinclair, 1979). However, grass growth on the control site did not concur with these expectations; productivity declined marginally with a drop in topography. Furthermore, since all litter was removed from exclosures at the beginning of the experiment, it is probable that productivity recorded in lower areas was unrepresentatively high. Studies by Kucera and Ehrenreich (1962) and Hulbert (1969) indicate that excessive amounts of litter depress productivity, presumably by shading sunlight and intercepting precipitation.

That productivity failed to explain topographic trends in phytomass emphasizes the importance of grazing. Distribution of cattle on the Ranch favors upper areas where grass is generally more nutritious and herdsmen do not have to contend with dense stands of thorny trees. Exacerbating this disparity are the preferences of Thomson's gazelle and wildebeest for upper topographic levels on the Athi Plains (Chapter 4; Owaga, 1975; Reed, 1983). Collectively, these three species comprise over 85% of the ungulate biomass at WRR. McNaughton (1979) contends that grazing stimulates grass productivity by enhancing

Table 5.6. Effect of Fire B on distribution of native ungulates (values represent number of sightings of animal groups).

		Burn Strip		Control Strip		T-test
	N	X	se	X	se	
Before Treatment	8	7.6	1.5	6.0	1.4	NS
After Treatment	8	12.5	2.0	5.1	1.0	<0.01

photosynthesis, tillering and nutrient recycling and by improving light conditions. By maintaining upper areas relatively free of litter, moderate grazing pressure can encourage grass growth by reducing competition for space, light and water. The input of urea into the soil from ungulates may be particularly important, as nitrogen commonly limits productivity throughout semi-arid Africa (Whiteman, 1980). In support, grass protein levels were highest in the upper levels of the burn and control sites.

From the above observations it is proposed that topography, by affecting such factors as ungulate mobility, forage quality and heat balance, influences patterns of resource use within the ungulate community. First, ungulates may avoid lower areas during the wet months because slippery conditions prevent firm footing and reduce escape speeds. Unlike the sandy hilltops, the clay-dominated depressions become swollen and sticky when wet, noticeably encumbering movement. Talbot and Talbot (1963) and Anderson and Herlocker (1973) indicate that large herbivores avoid heavy textured soils during the rainy season.

Secondly, the relaxed level of grazing in depressions during the rainy season enables grasses to progress to a tall senescent stage. This phytomass accumulates as litter which chokes new growth (Heady, 1956). Mature grasses are generally avoided by grazers since they are coarse, unpalatable and maintain lower levels of moisture, protein and digestibility than new growth (Afolayan and Fafunsho, 1978). Ungulates grazing in depressions would need to be highly discriminatory and unconstrained by time to sort through large amounts of unpalatable litter to find and ingest sufficient forage. In the Serengeti, McNaughton (1979) concluded that tall stemmy grasses are favored where grazing intensity is low since they can compete more effectively for light by overtopping more prostrate species. Low-growing stoloniferous plants are better adapted to intense grazing since the apical meristems are protected from herbivory and they reproduce vegetatively. This was precisely the pattern recorded; *Digitaria*, a prostrate perennial, was co-dominant in upper areas and was replaced by *Ischaeum* and *Pennisetum* in depressions. The low leaf/stem ratio and high lignin content render the tall grasses *Pennisetum* and *Ischaeum* of limited forage value (Reed, 1983). Talbot and Talbot (1963) have shown that wildebeest avoid mature swards of *Pennisetum* and actively search for shorter and more palatable forage. It follows that grazers would remain on upper slopes where actively regrowing grasses ensure high nutrient quality in the diet. It is not until later in the dry season, when grass growth ceases and available phytomass is depleted, that herbivores are forced to move downward to satisfy daily forage requirements.

Lastly, seasonal weather patterns necessitate a downward movement of ungulates in the dry season. As ambient temperature increases and moisture content in forage declines, water-dependent species must visit watering holes more frequently to meet physiological requirements. Research by Western (1975) in Kenya and by Afolayan and Ajayi (1980) in Nigeria indicate that seasonal movements of many ungulates species are best explained by availability of surface water and moisture content of forage. To accomodate shading behavior during periods of intense insolation, gazelles, wildebeest and hartebeest avoided treeless hilltops, preferring to stand or lie beneath *Balanites* and *Acacia* along lower slopes and depressions (pers. obs.).

As viewed by range managers, strong topographic-floral trends indicate an unbalanced grazing system which is predisposed to erosion along heavily grazed hilltops and where vast amounts of lowland phytomass advance to an undigestible phenological stage. Concerning this problem, fire appears to be an effective tool for creating a more uniform community structure. This study indicates that fire can significantly narrow or remove topographic disparity in phytomass, litter, leaf height and utilization. In effect, the lower burn levels adopt a vegetation structure similar to hill tops.

The drastic vegetation changes in lower burned areas can be traced to the amount of plant material present for combustion. Given the improved fuel characteristics of the depressions it is expected that fire intensity would increase with a drop in topography. Iwanami and Iizumi (1966) documented a positive relationship between the amount of litter cover present and maximum fire temperature. McArthur and Cheney (1966) contend that fire intensity increases in a linear fashion with available fuel.

Whereas numerous studies have shown fire to stimulate primary productivity by removing litter and the senescent standing crop and encouraging nutrient recycling (see Norton-Griffiths, 1979), no favorable response was recorded in this study. In a review of the North American literature, Harris (1972) noted that grass fires generally depress plant growth in areas receiving less than 500 mm of annual rainfall, while enhancing productivity in a linear fashion where precipitation exceeds 500 mm. A similar relationship has been shown for African grasslands by Daubenmire (1968). Explanations of this trend identify water as a major limiting variable below 500 mm of rain, while space constrains productivity in more moist sites. Whereas fire reduces competition for space it is often at the expense of increased evaporative losses of water. The results of this study are consistent with Harris's findings, since no effect was recorded for an area receiving approximately 500 mm of rainfall.

Although the effects of fire on nutritional quality of forage plants are largely conflicting, there are some well-documented studies indicating that fire increases ash and protein while decreasing fiber (see Daubenmire, 1968). Attempts to account for the variable findings stress the importance of such factors as season of burning, frequency and intensity, and post-fire climatic conditions on the resulting quality of forage. That fire did not improve the chemical composition of post-fire growth in this study might account for the similarity in primary productivity between treatment and control sites.

In general, range fires are considered useful for discouraging the encroachment and recruitment of unwanted woody species on livestock rangeland (Buechner and Dawkins, 1961; Phillips, 1965; Langlands, 1967; Scott, 1971). This study suggests that fire is an effective control agent on the low growing *A. drepanolobium*, but does not increase mortality rates for the tall *Balanites*. Similar results were reported by Norton-Griffiths (1979) and Pellew (1983), who documented a negative relationship between tree height and fire-induced mortality. Since a high proportion of the fire-killed stems exhibited coppicing, repeated burning would be required to ensure mortality. The relationship between topography and fire intensity underscores the need for sufficient grass fuel to ensure tree mortality. WRR management should consider the importance of trees for providing shade to ungulates when devising a prescribed burning program.

The literature is replete with examples of African ungulates being attracted to areas which have been recently burned (Brynard, 1964; Pratt, 1967; Lemon, 1968; Oliver, Short and Hanks, 1978; Rowe-Rowe, 1982) Since the fire treatment did not enhance nutritive quality for current years growth, other factors must be responsible. The most apparent difference concerns the functional distinction between available phytomass and usable forage. On the control site, particularly the lower sections, much of the acceptable forage is physically incorporated into or overlaid by unpalatable grass material of several years antiquity. Furthermore, the thorny spines and low spreading canopy of *Acacia* protects much of the underlying forage resource by discouraging herbivory. In contrast, nearly all graminaceous phytomass on the burn site was less than one year old. Grazing on the burn site was relatively uncomplicated since phytomass was uniform in height, moisture content, utilization and phenological stage across the topographic gradient. Furthermore, the high grazing pressure maintained the grass sward in a productive state by discouraging litter and promoting nutrient recycling and an optimal root/shoot ratio. An additional attractant was the greater amount of herbaceous cover created by a lower *Acacia* density.

For effective management, fire size demands consideration. Small burns can attract such high herbivore densities that vegetation is subjected to excessive grazing pressure and not given adequate rest to allow nutrient and tissue replenishment. If neglected by herbivores, non-burn areas will adopt a coarse structure refractory to subsequent grazing. A minimum burned area is needed to attract gregarious species of large size. For example, wildebeest were not recorded on the smaller experimental burn in numbers representative of their population; yet they strongly selected the larger burn.

5.5 Summary

Topographic relief imposes strong gradients in plant community structure by affecting soil moisture and physico-chemical properties. Proceeding downhill, quality and availability of grass forage decreases because of increased amounts of senescent phytomass, litter and incidence of *Acacia*. Native ungulates appear to avoid lower areas during wet periods perhaps because of impaired mobility. The resultant heavy grazing pressure on upper slopes ensures that grass remains in a nutritious regenerative state until moisture deficits occur in the dry season. As the dry season progresses and forage is depleted in upper sections, native ungulates move downhill to meet daily forage intake requirements. This movement may also be a thermoregulatory strategy, enabling ungulates to take advantage of shade offered by trees along hill sides and depressions.

In the context of the above relationships, fire represents a powerful force capable of homogenizing topographic-floral relationships by combusting moribund phytomass in depressions and by discouraging tree growth. Native ungulates concentrated on all topographic levels of recently burned areas. Major attractants include a vegetation structure conducive to grazing (i.e. short sward of actively regrowing tillers) and a reduction in trees which compete for moisture and light with grasses and discourage grazing by presenting a physical barrier. If soil moisture is adequate, heavy grazing pressure may perpetuate vigorous growth by preventing the accumulation of photosynthetically inactive material.

It would appear that a prescribed burning program is a useful management tool for maintaining primary productivity and promoting a more balanced use of forage resources by ungulates.

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5.7 Appendix

Appendix 5.1. Comparisons of step-point transects and ocular estimates of selected plant community characteristics.

	Number of Comparisons	Correlation Coeff. (R)	Significance F-Statistic	Slope	Y-intercept
Phytomass (g/m^2)	55	0.91	<0.01	0.97	19.0
Leaf ht. (cm)	18	0.85	<0.01	0.93	1.2
Grass utilization (%)	18	0.96	<0.01	0.95	0.1
Herbaceous Cover (%)	18	0.65	<0.01	0.73	25.4

Chapter 6

Effects of Livestock Enclosures (Bomas) on East African Rangeland Ecology

6.1 Introduction

Bomas (brush-ringed or fenced paddocks) are conspicuous features of African rangelands used by pastoralists for nightly protection of cattle, sheep and goats. Thomson's gazelle (*Gazella thomsonii*), Grant's gazelle (*Gazella grantii*), Coke's hartebeest (*Alcelaphus buselaphus*), wildebeest (*Connochaetes taurinus*) and other wild ruminants often frequent rangeland immediately surrounding abandoned bomas (Reed, 1983). Since nitrogen and phosphorus limit primary productivity in semi-arid regions of Africa (Whiteman, 1980), the influx of nutrients into boma areas from manure and urine, and the accompanying intense trampling and foraging, would be expected to modify the environment, creating a small yet distinctive community.

A study was conducted at Wildlife Ranching and Research Ltd. between September 1981 and June 1983 to quantify the effects of bomas on soil nutrient status, plant species composition and forage quality, production and utilisation.

6.2 Methods

Boma #1 was situated at the top of a topographic sequence in the western region of the Ranch. During the dry seasons, cattle visited the area daily to water from a nearby borehole. Pumped water was confined to the holding tank and watering trough and was therefore not thought to supplement soil moisture.

On September 8, 1981, three 1x1x1 m exclosures and three 1x1 m unprotected plots were located randomly within 10 m of a stake positioned 25 m from Boma #1. Similar protected and unprotected plots were located in a control area 250 m from the boma. All plots were clipped within 2 cm of ground level at the beginning of the study. At monthly intervals, green phytomass within each plot was estimated photometrically using a calibrated Tektronics J-16 spectral radiometer. Measurements were not made when green phytomass dropped below an estimated one-third of total phytomass as Boutton and Tieszen (1983) have shown the discriminating properties of the radiometer to be poor in this range. One year after the beginning of the experiment, each plot was reclipped to 2 cm height. All samples were air-dried (drying oven unavailable), sorted by species, weighed, then analyzed for nutrient quality. Plant fiber (m-ADF) and crude protein were determined according to methods outlined by Horowitz (1980). Three soil samples were randomly extracted from a depth 0-30 cm from the boma and control sites. Chemical analyses conducted by Norwest Soil Research Ltd., Edmonton, Canada followed McKeague (1978) except for HP_2O_4 and K which followed Hamm, Radford and Halstead (1970).

Three additional boma sites (#2,3 and 4) were studied in June 1983. Step-point transects were conducted at each boma and control site to quantify plant community structure. A thin incremented pin was lowered to the ground at each of 25 steps along eight transects originating at a central stake and oriented in ordinal and subordinal directions. This yielded a total of 200 points per sampling site and provided objective data on species composition, herbaceous cover, plant phenology, utilization and leaf height. Within one meter of each transect, demarcated by string, all intact faecal groups identifiable as gazelline (Thomson's and Grant's gazelles) or alcelaphine (hartebeest or wildebeest) were recorded to compare ungulate use at boma and control sites.

6.3 Results

6.3.1 Soil

In comparison to the control, the soil in the vicinity of Boma #1 contained significantly higher levels of nitrate, phosphate, sulfate, calcium, salts and organic matter (Table 6.1).

Table 6.1. Chemical and physical description of soil at Boma #1

	NO_3	HPO_4	K	SO_4	Ca	Na	Mg	pH	Salinity	Organic matter (%)
	(--------------------ppm						-----------------)			
Boma										
$\bar{x}$	33	>60	>450	16	1743	58	379	7.4	0.62	2.0
se	14	0	0	4	33	19	28	0.2	0.16	0
Control										
$\bar{x}$	4	40	>450	3	1503	19	338	6.6	0.13	1.0
se	1	1	0	0	80	1	20	0.0	0.01	0
T-test	<0.10	<0.01	NS	<0.05	<0.05	NS	NS	<0.01	<0.05	<0.01

6.3.2 Vegetation

The stimulating influence of the short rains (October-December) and the long rains (April-June) on plant growth at Boma #1 was considerable (Fig. 6.1). Throughout the study, green phytomass was highest in the boma exclosures, followed by control exclosures, unprotected boma and finally unprotected control plots. Annual productivity and utilization were significantly greater at the boma (Table 6.2).

Nutritive analyses indicated that grasses at Boma #1 contained higher levels of protein and lower amounts of fiber than did control plants (Table 6.2). No significant differences existed for ash, copper, zinc, iron, manganese and selenium.

Grasses at Bomas #2,3 and 4 were characterized by significantly greater utilization ($p<0.01$) and lower leaf height ($p<0.01$) than control plants (Table 6.3). Relative to control sites, herbaceous cover was significantly lower in Bomas #3 and 4 ($p<0.01$) and higher for Boma #2 ($p<0.01$). Almost all plant material identified at each of the boma sites was *Cynodon nlemfuensis* (Table 6.4). In contrast, the control sites contained small amounts or no *Cynodon*, but were dominated by *Pennisetum mezianum, Themeda triandra* and *Digitaria milanjiana.*

At the beginning of the dry season (June 1983), the entire grass sward at Bomas #2,3 and 4 was undergoing active regrowth following defoliation (Table 6.5). Contrastingly, most of the control grasses had advanced to a senescent non-photosynthetic stage.

6.3.3 Ungulate Distribution

Ungulate faecal density was significantly higher at boma than control sites (Table 6.6). Gazelle faeces were more numerous at Bomas #3 and 4, whereas alcelaphine use was greater at Boma #2.

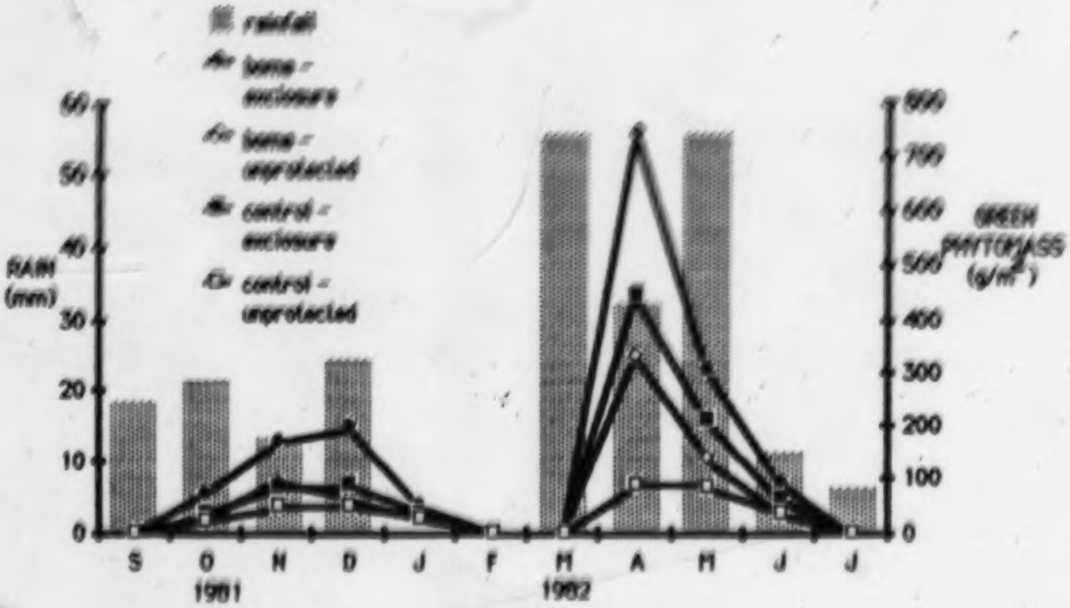

Figure 6.1 Effects of bomas, exclosures and rainfall on green phytomass at Boma #1.

Table 6.2. Production and nutritive quality of grasses at Boma #1.

	Productivity (g/m^2)		Utilization (%)		Fiber (m-ADF, %)		Crude Protein, %	
	X	se	X	se	X	se	X	se
Boma	465	84	100	0	35.1	1.9	8.0	0.8
Control	266	46	55	9	40.6	0.5	4.6	0.4
T-test	<0.10		<0.01		<0.05		<0.05	

Table 6.3. Plant community structure.

	Boma #2		Boma #3		Boma #4	
	X	se	X	se	X	se
Herbaceous cover (%)						
Boma	89.0	2.6	50.5	4.0	50.5	2.7
Control	70.5	4.5	77.5	2.7	79.0	2.7
T-test	<0.01		<0.01		<0.01	
Leaf height (cm)						
Boma	6.5	0.7	4.8	0.2	3.7	0.3
Control	26.8	3.7	10.7	0.7	10.6	1.2
T-test	<0.01		<0.01		<0.01	
Utilization (%)						
Boma	99.4	1.8	96.7	6.6	100.0	0.0
Control	12.8	11.8	47.1	4.7	62.5	4.3
T-test	<0.01		<0.01		<0.01	

Table 6.4. Plant species composition.

	Boma *1	Boma*2	Boma *3	Boma *4
Cynodon				
Boma	100	99	100	100
Control	0	0	10	0
Themeda				
Boma	0	1	0	0
Control	8	35	24	26
Pennisetum				
Boma	0	0	0	0
Control	87	18	20	51
Digitaria				
Boma	0	0	0	0
Control	5	25	28	0
Others				
Boma	0	0	0	0
Control	0	22	18	23

Table 6.5. Plant phenology in June 1983 (percent of plant community in each phenological class).

	Boma #2	Boma #3	Boma #4
Class 7			
Boma	0	0	0
Control	0	5	11
Class 8			
Boma	0	0	0
Control	1	13	40
Class 9			
Boma	0	0	0
Control	53	28	41
Class 10			
Boma	100	100	100
Control	46	54	8

Legend: Class 7. Unforaged; 25-50% of leaves dry
Class 8. Unforaged; 50-75% of leaves dry
Class 9. Unforaged; 75-100% of leaves dry
Class 10. Foraged; plant actively growing

Table 6.6. Faecal density (average */transect).

	Boma *2		Boma *3		Boma *4	
	X	se	X	se	X	se
Gazelline						
Boma	3.9	0.9	3.5	0.8	11.1	1.6
Control	4.3	1.0	0.9	0.5	1.6	0.4
T-test	NS		<0.05		<0.01	
Alcelaphine						
Boma	10.9	1.5	0.1	0.1	1.5	0.3
Control	1.3	0.6	0.3	0.2	1.1	0.4
T-test	<0.01		NS		NS	
Total						
Boma	14.8	1.4	3.6	0.9	12.6	1.6
Control	5.6	0.9	1.2	0.5	2.7	0.6
T-test	<0.01		<0.05		<0.01	

6.4 Discussion

The study indicated that bomas had profound effects on soil, flora and fauna. The addition of limiting nutrients, particularily nitrogen, from ungulate manure and urine enhanced soil fertility in the vicinity of the boma. Stimulatory effects of excreta on grass productivity have also been recorded by Peterson, Woodhouse and Lucas (1956), Lotero, Woodhouse and Peterson (1966) and Weeda (1967). Although not observed in this study, undesirable short term effects of excreta might include lower utilization of fouled herbage (Marsh and Campling, 1970) and temporary levels of ammonia which are toxic to plants (Doak, 1952).

The prevalance of *Cynodon* at bomas can be attributed to its preference for disturbed fertile areas (Dougall and Glover, 1964; Reed, 1983). Within the study area, it is only in these sites that *Cynodon* competes favorably with the dominant grasses *Themeda, Digitaria* and *Pennisetum*. It is difficult to speculate on the relative importance of soil enhancement and trampling in maintaining the competitiveness of *Cynodon* over other species. The low growing and stoloniferous nature ideally suit *Cynodon* to intense foraging and trampling pressure.

Intense ungulate use of the bomas, as evidenced by high faecal density and grass utilization and low leaf height, can be traced to *Cynodon*'s higher protein content and leaf/stem ratio and lower lignocellulose content (modified acid detergent fiber). *Cynodon* is widely recognized as one of the grasses most preferred by ungulates in East Africa (Pratt and Gwynne, 1977). The ability of animals to discriminate quantitative and qualitative differences in available food resources is an underlying assumption of optimal foraging theory (Schoener, 1971). Resource use studies have shown that African ungulates can detect and respond to spatial and temporal changes in nutrient status, plant phenological stage and species composition (Stewart and Stewart, 1970; Owaga, 1975; Owen-Smith, 1979).

Cynodon remained in a productive growth stage longer into the dry season than grasses in surrounding areas, accounting for the recorded higher annual productivity. Not discounting the importance of soil nutrient enrichment, the role of grazing on productivity should not be ignored. McNaughton (1979) has shown that moderate levels of foraging may maximize productivity through compensatory growth by encouraging an optimal root/shoot ratio, improving light reception by removing excessive litter, by applying growth-stimulating saliva and through hormonal redistribution promoting tillering.

The environmental impacts of bomas suggest management implications. To ensure redistribution of livestock and wildlife excreta throughout the rangeland, bomas should be relocated frequently. This would minimize local tracking and erosion, encourage balanced range use, and apply limiting nutrients over a larger area. Establishment of new bomas could be used to attract wildlife to underutilized rangeland.

The effects of bomas appear to persist. Several small round patches of *Cynodon* were found which had no recent history of livestock confinement. It is possibly that these sites are the relics of bomas from an earlier management era dating back at least 15 years. For example, *Cynodon* dominated a small area near the remains of buildings constructed early in the century. Perpetuation of this unique microhabitat might be the result of *Cynodon* attracting grazers, which in turn maintain *Cynodon* by increasing soil fertility and by discouraging less prostrate species through trampling.

6.5 Summary

Abandoned livestock enclosures (bomas), and their immediate vicinity, were biophysically distinct from surrounding rangeland. The input of considerable amounts of excreta from ruminants, and the resultant soil enrichment, increased productivity of grasses characterized by high protein, low fiber and a prolonged growing season. As evidenced by faecal density and grass utilization, native ungulates strongly preferred boma sites. By encouraging compensatory growth of grasses, moderate to high use of boma vegetation might increase productivity and maintain the plant community in a more nutritious state.

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Chapter 7

Body Condition of Thomson's and Grant's Gazelles in Relation to Seasonal Environments and Resource Use

7.1 Introduction

The acute seasonality in rainfall that characterizes East Africa (Pratt and Gwynne, 1977) imparts equally noticeable trends in plant community structure, particularly forage quality and biomass (UNESCO, 1980). During periods of adequate soil moisture, grazing ungulates experience a nutritious forage regime characterized by relatively high levels of protein, moisture and digestibility (Dougall, Drysdale and Glover, 1964; Afolayan and Fafunsho, 1978; Snaydon, 1981). Although phytomass may remain high in the dry season, grass quality deteriorates quickly through lignification and losses in protein and moisture (Duncan, 1975; Field, 1975).

Sinclair (1975) argued convincingly that the poor quality of dry season forage is a major factor limiting African ungulate populations. During this season, the nutritional plight of ungulates is exacerbated by heat stress and a shortage of drinking water. To balance increases in evaporative cooling, most ungulates allocate more time to shading behavior, and moving to and from water (Wilson, 1961; Sinclair, 1977).

Although animals buffer themselves against seasonal changes by altering resource use patterns and invoking physiological adaptations, the limits of adaptive plasticity may be constrained by interspecific competition and evolutionary history.

Given seasonality in environmental quality and ecological separation within African ungulate communities (Bell, 1970; Leuthold, 1978), I predict that ungulates will exhibit seasonal variations in body condition and that species exploiting different ends of resource spectra will vary in body condition asynchronously. The species chosen to test this hypothesis are the Thomson's gazelle (*Gazella thomsonii*) and Grant's gazelle (*Gazella granti*). Although similar in general appearance and social structure (Walther, Mungall and Grau, 1983), these species display contrasting patterns of resource use (see Chapter 4).

7.2 Methods

7.2.1 Meteorology

Precipitation was measured monthly from a central location on the study site. Relative humidity and dry bulb temperature were monitored between October 1981 and December 1982.

7.2.2 Resource Use Behaviour

A 34 km circuit of existing tracks, encompassing all topographic levels and major vegetation types, was selected for monitoring resource use. Monthly surveys were conducted by motorcycle between September 1981-March 1982 and September-December 1982. For each ungulate sighting within the survey strip width, ocular estimates, calibrated to step-point transects (Appendix 5.1), were made for leaf height (average height of leaves in sward; cm), grass utilization (proportion of current years growth foraged), dicotyledon cover (%) and phenological stage. Topographic position (upper, middle and lower) and tree density (#/ha) were also recorded. Three randomly-placed 0.25 m^2 vegetation plots were clipped from a representative catena for each of the three topographic positions. All vegetative herbaceous material, both attached and litter were collected for weighing. Two samples were collected for nutritive analyses; the first in the dry season (August, 1982) and the second in the rainy season (November, 1982). Crude protein and fiber (m-ADF) were determined according to methods outlined by Horowitz (1980).

7.2.3 Body Condition

Between January 1981 and December 1982, body condition of adult male gazelles was monitored by recording the following index on harvested individuals (Thomson's gazelle, n=336; Grant's gazelle, n=190).

Kidney Fat Index (KFI) = 100 X perirenal fat (g)/head length (cm)

Perirenal fat is that adipose tissue (*capsula adiposa*) surrounding the kidney, weighed together with the *tunica fibrosa*. Head length, defined as the distance from the tip of the nose to the atlas joint measured along the dorsal curvature of the head, was chosen as an index of frame size which does not change with body condition. Although kidney weight has been used as a denominator (Riney, 1955; Hanks et al., 1976), it was rejected in this study because it covaried seasonally with kidney fat. Seasonal variation in kidney weight has also been documented for caribou (*Rangifer tarandus*) by Dauphine (1975) and waterbuck (*Kobus ellipsyprimus*) and Grant's gazelle (Spinage, 1984). To justify the use of kidney fat in comparing the condition of the two gazelles, it is assumed that location and sequence of tissue deposition and mobilization are similar in these two species.

Smith (1970) documented a highly significant relationship between kidney fat and total body fat for seven species of East African ungulates. Studies by Ransom (1965) and Sinclair and Duncan (1972) have shown that measures of bone fat are preferred to kidney fat as indicators of condition in more advanced stages of under-nutrition. The need to provide the retail market with intact carcasses prevented inspection of bone marrow.

7.3 Results

7.3.1 Climate

Four distinct rainy periods were encompassed by the study; heaviest amounts were received in March-April 1981 and October-December 1982 (Fig. 2.3). Driest periods occurred in June-August 1981, January-February 1982, and June-September 1982. Associated with rainfall, relative humidity was highest in the months of May and November and lowest in February and July. Temperatures peaked in February and March and were lowest in June, July and August.

7.3.2 Vegetation

For each topographic level, forage quality (crude protein/fiber) was highest in the wet season and lowest in the dry season (Table 7.1). Proceeding downhill, leaf height, tree density, and incidence of dicotyledons increased whereas grass utilization decreased (Table 7.1, Fig. 7.1). Grasses located in the upper topographic levels initiated growth earliest (Table 7.2) and contained highest levels of protein and lowest amounts of fiber (Table 7.1). In the depressions, accumulations of senescent grasses dominated well into the rainy season, while herbivores removed all, or most, phytomass on hilltops.

7.3.3 Ungulate Distributions

The two gazelle species displayed marked differences in topographic distribution (Fig. 7.2). Relative to the proportion of each topographic level in the road survey, Thomson's gazelle preferred upper areas whereas Grant's gazelle occupied lower sections. However, topographic use was strongly influenced by rainfall. Both species exhibited seasonal topographic migrations, moving upwards during wet periods and relocating downhill as dry conditions intensified.

7.3.4 Body Condition

Seasonality in body condition was pronounced for both species, with trends resembling the rainfall pattern (Fig. 7.3). Least-square regression indicated significant relationships between body condition and rainfall for both species. By statistically lagging and leading the kidney fat index, it was possible to explore the best temporal relationship of body condition to rainfall. When regressing kidney fat to rainfall, a 2 and 3 month lag explained the most variation for Thomson's ($r=.68$; $p<0.001$)) and Grant's gazelle ($r=.65$; $p<0.001$), respectively. Similarly, correlation analyses between species indicated that body condition of Grant's gazelle lagged 1 month behind that of Thomson's gazelle ($r=.69$; $p<0.001$).

Table 7.1. Effects of topography and/or season on grass crude protein, fiber, tree density and dicotyledon cover in 1982.

	Crude Protein (%)		Fiber (%)		Tree Density (#'s/ha)		Dicotyledons (%)	
	dry (Aug.)	wet (Nov.)	dry	wet	X	s.e	X	s.e.
Upper	6.37	11.83	45.3	37.0	11.2	1.3	0.5	0.1
Middle	2.87	5.71	52.5	49.0	44.2	4.7	1.1	0.2
Lower	2.63	4.80	54.7	52.9	107.0	7.4	2.3	0.6

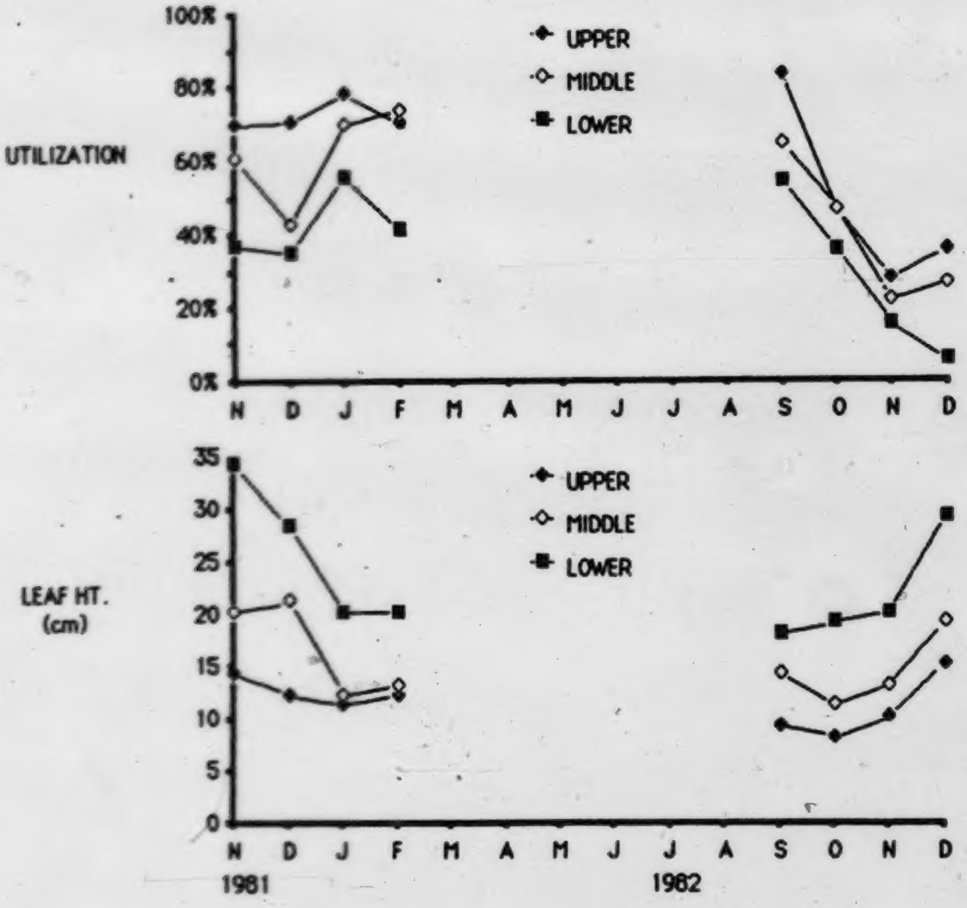

Figure 7.1 Effects of topography and season on grass utilization and leaf height.

Table 7.2. Effect of topography on percent of tillers actively growing (data for 1982).

	Sept.	Oct.	Nov.
Upper	4.1%	49.9%	100%
Middle	2.2%	37.0%	100%
Lower	0.5%	12.1%	100%

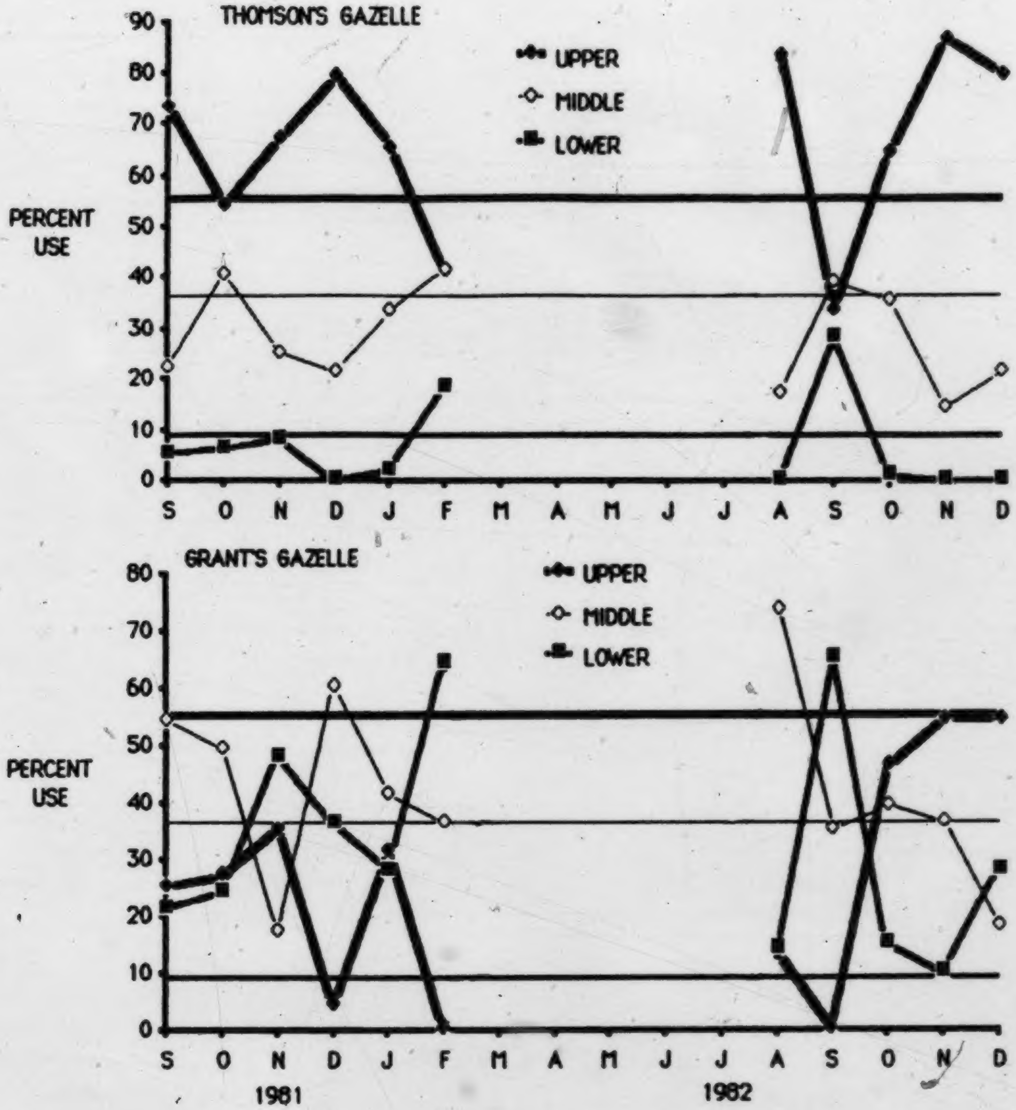

Figure 7.2 Patterns of resource use by Thomson's and Grant's gazelle. Horizontal lines (refer to the amount of each topographic level in the road survey (upper = thick, middle = thin and lower = medium) and indicate if animals prefer or avoid certain areas.

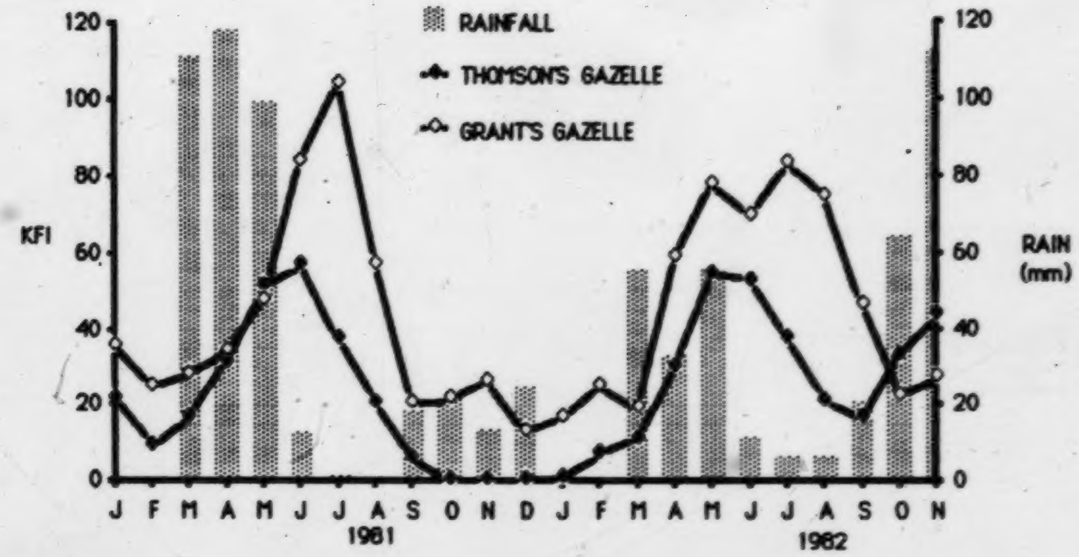

Figure 7.3 Body condition of Thomson's and Grant's gazelle, as measured by Kidney Fat Index = 100 X perirenal fat (g)/head length (cm). KFI values represent running means.

7.4 Discussion

The results suggest that body condition of male gazelles is affected proximally by forage quality, indirectly by animal distribution across topographic gradients and ultimately by rainfall patterns. Declines in forage quality and quantity recorded during the dry season were substantial. In the Serengeti ecosystem, Sinclair (1977) recorded a strong relationship between body condition and grass protein, and considered 5% crude protein to be a minimal level needed for maintaining condition in buffalo (*Syncercus caffer* Sparrman). In reviewing the literature, Robbins (1983) stated that ungulate protein requirements for maintenance range between 5.5-9.0 percent. Not discounting their ability to select nutritious plant parts, it seems unlikely that gazelles could maintain adequate levels of protein intake from grasses in the dry season. Although dry season protein levels may be marginally adequate along hilltops, available phytomass there was almost completely exhausted.

The study confirmed that resource partitioning existed between the two gazelle species; Thomson's gazelle preferred heavily utilized, sparsely treed hilltops, and Grant's gazelle occupied topographic depressions, characterized by dense stands of trees, tall grasses and abundant forbs. Despite topographic dissimilarity, both species exhibited seasonal topographic migrations, moving downward as dry conditions intensify in search of moist forage, surface water, browse, and trees for shading from meteorological stress. A shift in gazelle diet toward dicotyledons (Gwynne and Bell, 1968; Stewart and Stewart, 1970; Spinage, Ryan and Shield, 1980) increases protein intake since dicotyledonous plants maintain higher dry season levels of protein than grasses. Another factor encouraging a downward movement during the dry season is the paucity of forage available on hilltops and ridges.

I suggest that gazelles avoided lower areas during wet periods because slippery conditions prevent firm footing and reduce escape speeds. Unlike the sandy hilltops, the clay-dominated depressions become swollen and sticky when wet, noticeably encumbering movement. Studies by Talbot and Talbot (1963) and Anderson and Herlocker (1973) indicate that large herbivores avoid heavy textured soil during the rainy season. As a further incentive to moving upward following rainfall, animals benefit from the homogenous sward of rapidly growing grasses.

Kidney fat for Thomson's gazelle appears to track rainfall closely. Adipose tissue is deposited rapidly following the rains, and mobilized early in the dry season. This species benefits from the floral "green-up" occurring on the heavily grazed hilltops immediately following the rains. The high protein content and early phenological stage of grasses along hilltops in the rainy season attest to the nutritious forage available. Contrastingly, Grant's gazelle maintain condition longer in the dry season. Located further down the catena, Grant's gazelle must contend with accumulations of senescent phytomass which obscure new shoots. One would expect topographic relief to maintain soil moisture longer in the depressions, which should in turn prolong the growing season. Therefore, I suggest that forage quality may peak progressively later as one proceeds downhill and this disparity accounts for the asynchronous body condition pattern observed between the Thomson's and Grant's gazelle.

It might be argued that observed fluctuations in body condition of gazelle reflect involvement in rutting behaviour, as has been documented for ungulate species which breed seasonally (Sinclair and Duncan, 1972; Duncan, 1975; Dunham and Murray, 1982). For Thomson's and Grant's gazelle, it is assumed that reproductive cycles do not greatly bias trends in body condition, since territorial males and neonates were observed each month of the year.

Lowest levels of peri-renal fat were recorded during October 1981 - February 1982; a period characterized by sub-normal precipitation and very high temperatures. Thomson's gazelle, which depleted all peri-renal fat for a 4 month period, were in poorer condition than Grant's gazelle. This difference may reflect the greater use of high protein forages (dicotyledons) and the lower dependency on water by Grant's gazelle (Taylor, 1968).

These findings may prove helpful to a game rancher in that they suggest predictable seasonality in body condition. By structuring the harvesting schedule to concentrate on animals in good condition, a staggered harvest of Thomson's and Grant's gazelle could increase carcass yield.

7.5 Summary

A bimodal rainfall pattern and topographic relief were identified as major determinants of forage availability and quality on the Athi-Kapiti Plains, Kenya. Body condition of male gazelles, measured by perinephric fat, fluctuated seasonally in response to changes in environmental quality. Preferences for upper topographic levels by Thomson's gazelle and for depressions by Grant's gazelles exposed these species to dissimilar conditions and accounted for asynchronous trends in body condition. Thomson's gazelles benefitted from the early floral greenup which occurred along hilltops immediately following the rainy season. Body condition of Grant's gazelle was maintained longer into the dry season because of the abundance of dicotyledons and persistence of soil moisture in topographic depressions.

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Chapter 8

Relationships Among Physical Traits, Age and Social Status in Thomson's and Grant's Gazelles

8.1 Introduction

Size and conformation of the bovid body and horns are thought to be primary determinants of social dominance and hence access of males to estrous females (Geist, 1966; Jarman, 1974; Leuthold, 1977; Walther, 1978a; Kingdon, 1982). Since social status is established through ritualized combat and intimidation displays, physically impressive males are expected to dominate agonistic encounters and contribute disproportionately to the gene pool. Although this relationship is generally accepted, and has been documented for bighorn sheep (Geist, 1971), morphometric differences among African bovid males of different social status have not been adequately studied.

In conjunction with the commercial game cropping program at WRR, a study was undertaken to determine if males of different social status were dissimilar in size, conformation and age. The species chosen for study were two antilopines; the Thomson's gazelle (*Gazella thomsonii*) and Grant's gazelle (*Gazella granti*). Both species possess a social structure consisting of three subgroups; territorial males, female groups and bachelor herds (Estes, 1967; Walther, Mungall and Grau, 1983). I assume that the distinction between bachelor and territorial males offers a satisfactory measure of social and reproductive status. Among territorial individuals, males accompanying female groups were distinguished from solitary males to identify possible age and physical differences which might explain associations with females.

Territorial males defend areas from other adult male conspecifics. It is generally believed that territory holders constitute the male breeding sector and that the most "fit" individuals occupy preferred areas (Leuthold, 1977). Female groups include females of all ages and their subadult offspring. Young males generally leave this group at adolescence with progressive harassment from territorial males. Bachelor groups consist exclusively of males which range in age from adolescent to very old. It is within this group that subadult males complete most of their body growth, develop the behavioral and combative skills needed to enhance their social standing and, where competition is intense, exhausted older males regain strength before resuming territorial status. Although not empirically demonstrated, it is assumed that dominant individuals in bachelor groups are the most likely candidates to become territorial through displacing incumbents or by establishing new territories. Bachelors avoid territorial males and are therefore relegated to sub-optimal habitat (Kiley-Worthington, 1965; Estes, 1969,1974; Gosling, 1974).

8.2 Methods

8.2.1 Data collection

During weekly night cropping operations between September 1982 and August 1983, social status of 70 male Thomson's gazelle and 30 male Grant's gazelle was identified. Criteria used to identify social groups were:

Bachelor - male accompanied by one or more other males.

Territorial - adult male not accompanied by other males.

Harem - Territorial male escorting a female group.

Solitary - Lone territorial male.

Walther, Mungall and Grau (1983) questioned the accuracy of the term "harem", noting that associations between female groups and territorial males are transient. Since gazelle males are generally unsuccessful at confining females within territory boundaries, the status of territorial males (harem versus solitary) shifts repeatedly as female groups move across a mosaic of territories. An effort was made to collect representatives from each social group monthly. With a bright spotlight, it was possible to immobilize the target animal and to search the vicinity for other individuals which would indicate his social status. Individuals were excluded from the analyses when the vehicle noticeably disrupted group structure or there was uncertainty concerning group identity.

Harvested animals were transported to a nearby abbatoir where an array of measurements were taken. Animals collected after November 1982 were aged using patterns of tooth eruption and wear as outlined by Sinclair and Grimsdell (1978) and modified for the study population by Allen (1982). Dental criteria used for identifying age groups are presented in Appendices 8.1 and 8.2.

Body length, shoulder height, horn length, its base circumference and spread at tip, and carcass weight were measured (Table 8.1). These parameters were selected to reflect the conformation of the individual in terms of frame size, head adornment and body weight, respectively.

8.2.2 Data analysis

Initially, body characteristics and age of bachelor and territorial males were compared. Next, morphometric differences between the two territorial subgroups, solitary and harem, were explored for Thomson's gazelle. Insufficient numbers of territorial Grant's gazelle were measured to provide a meaningful comparison of solitary and harem individuals. Univariate analysis of variance was applied to each morphometric parameter and then all data were analyzed by multiple discriminant analysis to identify gradients of variation which best expressed morphometric differences among the social groups. Computations began with a data set consisting of N measurements (70 T. gazelle, 30 G. gazelle) on 6 morphometric parameters from individuals belonging to 2 or 3 social groups. Using linear combinations of the original morphometric parameters, the data set was reduced to 1 or 2 orthogonal and linear functions. The relative contribution of the original dependent variables is indicated by the standardized coefficients of the discriminant functions. The computations were executed using the subprogram DISCRIMINANT of the SPSSx statistical package (Nie, 1983).

Table 8.1. Morphometric variables used in comparison.

Category	Description
Body length (cm)	From atlas joint to base of tail, measured directly above vertebral column.
Shoulder height (cm)	Measured from highest point on the whithers to the tip of hoof following the curves of the shoulders in a straight line.
Carcass weight (kg)	Weight of eviscerated carcass; skin, head and lower legs removed.
Horn length (cm)	Distance between base and tip of horn measured along frontal surface.
Tip to tip length (cm)	Distance between horn tips.
Horn circumference (cm)	Measured around the base of the horn.

8.3 Results

8.3.1 Thomson's gazelle

Carcass weight and horn characteristics were significantly greater for territorial than bachelor males, whereas skeletal measures (i.e. body length and shoulder height) did not differ (Table 8.2). In comparing the two territorial subgroups, harem males were lighter than solitary males. Fig. 8.1 depicts the age distribution of males from each group. Territorial males were significantly older ($p<0.01$) than bachelors, as were harem males over solitary individuals ($p<0.05$).

In comparing bachelor, solitary, and harem individuals using canonical analyses, two discriminant functions (DF) were derived (Fig. 8.2). Standardized coefficients for each of the canonical variates optimizing discrimination among the three social units are contained in Table 8.3. The major contributing variable to DFI was horn length, which discriminated bachelor from territorial males. DFII was dominated by carcass weight which distinguished the more heavily-bodied solitary males from the lighter harem individuals.

8.3.2 Grant's gazelle

Relative to bachelor males, territorial individuals possessed longer horns and were significantly heavier (Table 8.2). Frame dimensions (height, length) did not differ significantly. Bachelors were significantly younger ($p<0.05$) than territorial conspecifics (Fig. 8.1).

A single permissible discriminant function explained 72% of the among group variation between bachelor and territorial individuals. The major contributing variables to this function were horn length and carcass weight (Table 8.3).

Table 8.2. Morphometric measurements from gazelle males of different social status.

		Body Length		Shoulder Height		Carcass Weight		Horn Length		Tip to Tip		Horn Circum.	
	N	X	se	X	se	X	se	X	se	X	se	X	se
Thomson's gazelle													
Bachelor	20	75.5	1.0	64.4	1.0	11.1	0.4	19.6	1.0	8.2	0.5	8.8	0.3
Territorial	50	78.1	0.8	66.3	0.4	12.8	0.2	28.3	0.3	9.4	0.2	9.9	0.1
F-statistic		N.S.		N.S.		<0.01		<0.01		<0.05		<0.01	
Solitary	37	77.9	1.0	66.3	0.5	13.0	0.2	28.6	0.3	9.2	0.3	10.0	0.2
Harem	13	78.5	1.4	66.4	0.9	12.2	0.4	27.5	0.9	9.9	0.5	9.8	0.4
F-statistic		N.S.		N.S.		<0.05		N.S.		N.S.		N.S.	
Grant's gazelle													
Bachelor	12	104.3	1.9	93.3	1.7	30.1	1.4	40.2	2.9	21.8	2.5	15.4	0.7
Territorial	18	104.6	1.0	96.1	0.9	36.0	0.7	51.3	1.1	26.6	1.3	15.9	0.4
F-statistic		N.S.		N.S.		<0.01		<0.01		N.S.		N.S.	

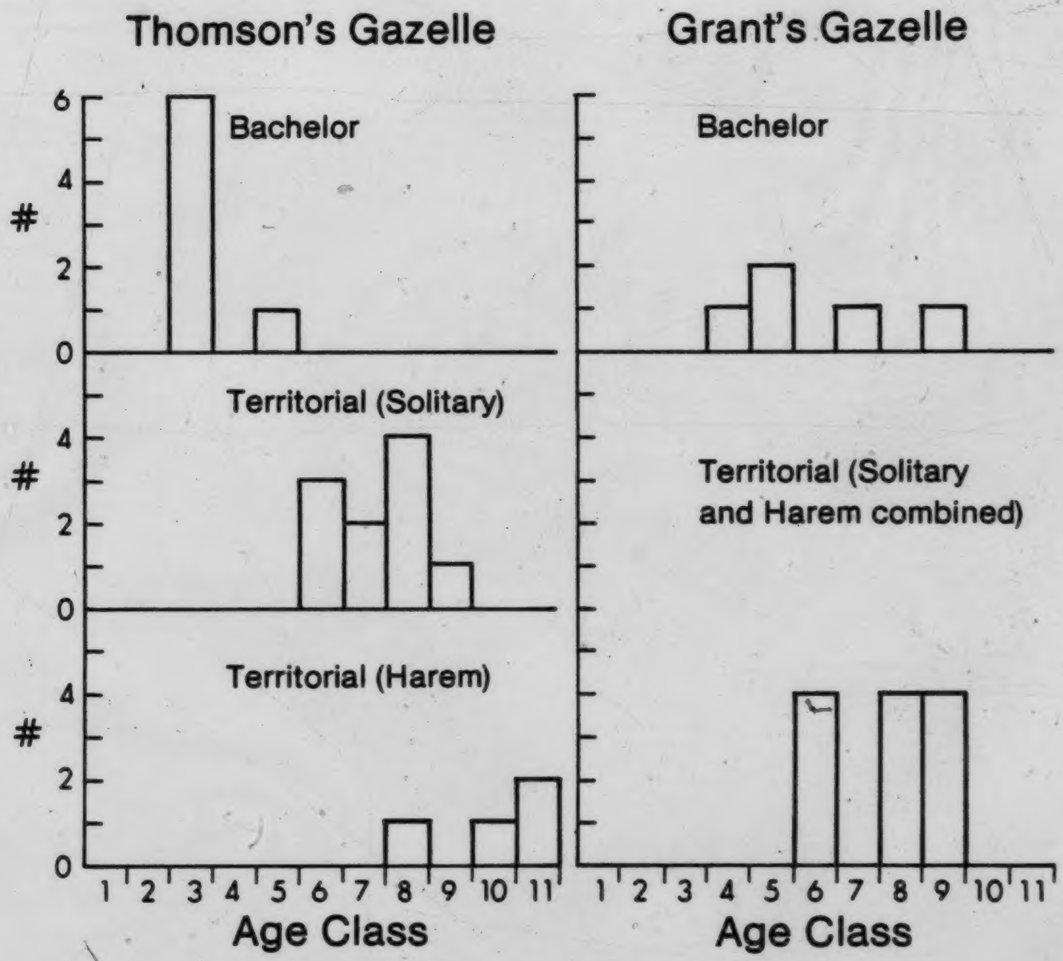

Figure 8.1 Age distribution of gazelle males from different social groupings.

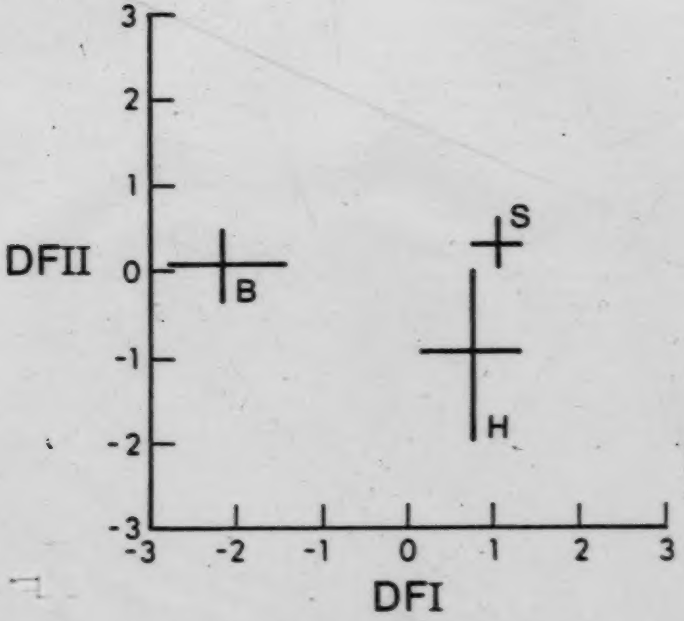

Figure 8.2 Morphometric differences between three social groups of Thomson's gazelle. Location of group centered (+/- 2 SE) according to two canonical variates; B, bachelor; S, solitary; H, harem.

Table 8.3. Discrimination among social groups on the basis of morphometric parameters. Standardized function coefficients and the canonical correlation of each function are given.

Variables	Thomson's gazelle Function I	Thomson's gazelle Function II	Grant's gazelle Function I
Body Length	-0.19	-0.27	-0.42
Shoulder Height	-0.44	-0.33	0.38
Horn Length	1.22	-0.30	0.54
Tip to Tip	-0.29	-0.67	-0.23
Horn Circ. at Base	0.08	0.11	-0.36
Carcass Weight	0.07	1.18	0.75
Canonical Correlation	82.4	43.5	72.3

8.4 Discussion

Bachelor and territorial males differed substantially in size and conformation. All bachelor males of Thomson's gazelle were younger than territorial conspecifics, suggesting that young males were unable to establish territories. This is in agreement with Walther (1978b) who concluded that subadult male Thomson's gazelle are incapable of maintaining territories because of deficiencies in physique and behavioral prowess. The absence of physically mature males in the bachelor groups suggests that older individuals were not abandoning established territories, either voluntarily or by displacement, and returning to non-breeding bachelor groups. This might reflect the low density of males and the attendent reduction in agonistic interactions.

An alternative explanation concerns the absence of "old" male Thomson's gazelles from all social groups. Using the ageing criteria of Robinette and Archer (1971), the oldest males harvested in this study were three years. That males were not surviving to advanced age can be attributed to the intense and selective removal of males by the harvesting program. Inter-ranch movement of animals, and hence recruitment of outside males, was prevented by a game-proof fence which enclosed the Ranch.

Comparisons with Kingdon's (1982) morphometric figures indicated that the study area supports diminutive adult males of both Thomson's and Grant's gazelle. It is conceivable that morphometric differences between social groups would have been more pronounced in nearby unharvested populations. By maintaining low densities of males, mostly young or recently mature, the harvesting program prevented males from surviving to an age where they could express their genetic potential. The longterm effects of these population anomalies on gene pool heterogeneity deserve attention.

Although bachelor males of Grant's gazelle were younger than territory holders, some older individuals remained in the non-reproductive group. Since territory size for Grant's gazelle is greater than Thomson's gazelle by a factor of approximately ten (Walther et al. 1983), a full complement of incumbents may have prevented further recruitment and ensured competition. Using Spinage's (1976) ageing criteria (which were used for females), some males achieved ages of 6-7 years. This implies that older males in poor condition have been forced to abandon their territories by stronger and younger males or were incapable of ever attaining territorial status.

For both species, members of bachelor herds were characterized by mature frame dimensions, but were diminutive in horn size and muscle development. In contrast, territorial males portrayed a masculine physique characterized by mature horns and a rounded musculature. To what extent the lower carcass weight of bachelors reflects youth or relegation to areas of poor range conditions by aggressive territorial males is speculative. These data support the belief that horn dimensions are critical to the establishment of dominance because of their evolutionary emphasis in the intraspecific acts of display, fighting and defence (Geist, 1966; Walther, Mungall and Grau, 1983).

Although not as apparent as the above differences, the data indicate that the two territorial subgroups for Thomson's gazelles differ in some respects. The lower carcass weight of harem males, relative to solitary individuals, probably reflects differences in body condition. Involvement of harem males in energy-expensive breeding activities could deplete body reserves and sacrifice time available for foraging. Numerous studies (Buechner, 1961; Jarman and Jarman, 1973; Hanks et al., 1976) have documented substantial declines in body condition of reproductively active bovid males during the breeding season.

The greater age of harem males might indicate the value of experience to reproductive fitness. The age-related advantage could operate through accumulated knowledge in selecting and maintaining territories attractive to females. Perceived differences among territories in terms of male attractiveness or resource quality might account for the differential preference of female groups to certain areas.

Territorial male Thomson's and Grant's gazelles on WRR were older, heavier and possessed longer horns than bachelor conspecifics. Among territorial Thomson's gazelles, males accompanied by females were older than solitary individuals but differed little in frame and horn dimensions. Small sample sizes precluded similar analysis for Grant's gazelles. These results suggest the importance of size, age and perhaps experience in determining social status.

8.5 Summary

Measurements of conformation, size and age indicated that territorial male Thomson's and Grant's gazelles were older, heavier and possessed longer horns than bachelor conspecifics. These data support the contention that body morphometrics influence social status. Among territorial Thomson's gazelle, those males accompanying females were older than solitary individuals, suggesting the importance of experience to reproductive success.

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8.7 Appendix

Appendix 8.1. Dental criteria for ageing Thomson's gazelle[1].

Age Class	Description
1	M_1 erupted but not in wear
2	M_2 erupted but not in wear; M_1 in wear
3	M_1 and M_2 erupted and in wear; M_3 erupted but not in wear
4	Molar table fully in wear; M_1 infundibula separate and cup-shaped; rostral and caudal infundibula of M_2 and M_3 joined
5	M_1 and M_2 infundibula separate and cup-shaped; M_3 infundibula joined.
6	Infundibula of all molars separate and cup-shaped
7	M_1 infundibula sickle-shaped; M_2 and M_3 infundibula cup-shaped
8	M_1 infundibula are straight lines; M_2 and M_3 infundibula are cup-shaped
9	M_1 infundibula are spots; M_2 infundibula sickle-shaped; M_3 infundibula cup-shaped
10	Rostral infundibulum of M_1 absent; M_2 infundibula sickle-shaped; M_3 infundibula cup-shaped
11	Rostral and caudal infundibula of M_1 absent; M_2 infundibula sickle-shaped; M_3 infundibula cup-shaped

[1] Modified from Allen (1982)

Appendix 8.2. Dental criteria for ageing Grant's gazelle[1].

Age Class	Description
1	M_1 erupted but not in wear
2	M_2 erupted but not in wear
3	M_3 erupted but not in wear
4	Molar table fully in wear; M_1 and M_2 infundibula separate and cup-shaped; M_3 infundibula joined
5	M_1, M_2 and M_3 infundibula separate and cup-shaped
6	Rostral infundibulum of M_1 sickle-shaped; caudal infundibulum of M_1 and M_2 and M_3 infundibula cup-shaped
7	Rostral infundibulum of M_1 a straight line; caudal infundibulum of M_1 sickle-shaped; M_2 and M_2 infundibula cup-shaped
8	Rostral infundibulum of M_1 a spot; caudal infundibulum of M_1 a straight line; M_2 and M_3 infundibula cup-shaped
9	Rostral infundibulum of M_1 absent; caudal infundibulum a spot; M_2 and M_3 infundibula cup-shaped
10	Infundibula of M_1 absent; M_2 infundibula sickle-shaped; M_3 infundibula cup-shaped
11	Rostral infundibulum of M_2 a straight line; caudal infundibulum of M_2 sickle-shaped; M_3 infundibulum cup-shaped

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[1] Modified from Allen (1982)

Chapter 9

Conclusions

9.1 Applications of Research to WRR Management

The preceding research chapters identify several ecological and production relationships within WRR. This section intends to discuss the relevance of these interdisciplinary findings to resource management and to suggest measures that might increase productivity and economic viability.

The impressive growth rate in biomass density of 12%/yr recorded for native ungulates on WRR (Chapter 3), despite an annual offtake of 40%, has been attributed to an effective perimeter fence, reduced cattle numbers, predator control and a skewed sex ratio. There is reason to believe that sustained harvest can be increased by optimizing these management practices, and exploring others.

Further reductions in the cattle population would provide greater amounts of forage for native herbivores and promote recovery of rangelands adjacent to water and boma sites. However, caution must be exercised regarding the rate of herd liquidation. Accumulations of senescent phytomass between 1982-84 were blamed on insufficient numbers of herbivores to remove yearly plant production. Several management options exist which address this problem. Attrition of livestock numbers, in terms of metabolic biomass, could approximate the increase in native species. At the present growth rate of wildlife, cattle could be gradually reduced over the following 9-10 years, at which time the native ungulate community would achieve estimated carrying capacity. If WRR's financial status could withstand a reduction, or suspension of harvest rate, the transition period could be lessened.

Efforts to increase numbers of those herbivore species which prefer coarse grasses would partially alleviate the problem of unwanted phytomass. In particular, a large herd of zebra would provide an ecological replacement for a diminishing cattle population. Efforts to attract and drive zebra into WRR from surrounding rangeland in the late 1970's proved largely unsuccessful. Assuming that government permission for such captures could now be secured, new strategies would need to be employed.

As indicated in Chapter 5, prescribed burning has proven useful in removing excess plant litter from topographic depressions, thereby encouraging a more even topographic distribution of herbivores. The amount of rangeland that could be expediently burned would be determined by the dry season forage requirements of the existing herbivore populations and the desired level of browsers in the ungulate community. Dry season fires can drastically reduce forage at a period of poor diet quality and are detrimental to browsers by selectively killing shrubs and low growing trees. By promoting large areas of rapidly growing grasses following the rains, fire could be used as a managerial tool to attract herbivores from outside the Ranch.

The results of Chapter 6 suggest the managerial value of cattle enclosures (bomas) for attracting native herbivores to areas receiving light use. Frequent relocation of bomas would prevent excessive range degradation from herbivore trampling.

Another managerial option for increasing wildlife production is to reduce predator populations. In that conservation of natural resources is a pivotal objective of WRR (Hopcraft, 1980), intensifying predator control would create a philosophical dilemma. This well illustrates the potential conflicts of conservation strategies subjected to the monetary priorities of free enterprise. Given the low natural mortality indicated for native ungulates by the population dynamics model (Table 3.10), the economic benefits arising from intensifying predator control would be minimal. The existing policy on WRR seems to be a realistic approach to the problem; predators other than jackals are controlled only if livestock are killed.

The selective cropping of males, as quantified in Chapter 3, has resulted in a skewed sex ratio favoring females. Inspection of harvested females indicated that sex ratios approximating 10:1 have not detectably reduced pregnancy rates. To promote increased population growth, WRR may wish to explore optimal female/male ratios. The sex ratio at which pregnancy begins to decline could be ascertained by examining the reproductive tract of harvested females. However, there may be attendant losses in evolutionary fitness resulting from low numbers of breeding males, since population vigour, fertility and viability are decreased proportional to reductions in genetic heterozygosity (Frankel and Soule, 1981). Furthermore, loss of genetic information (alleles) is exacerbated when dominant males monopolize the breeding of several females. Such is the case for Thomson's and Grant's gazelles, hartebeest and wildebeest, the males of which maintain breeding territories for part of the year. In the example provided by the above authors, the amount of genetic information present in a zebra population of 100 consisting of 60 females, 12 stallions and 28 non-breeding bachelors equals that of 40 randomly breeding individuals. Although the sensitivity of each species to inbreeding depression is not known, WRR management should be concerned about the long-term effects of inbreeding. Efforts should be made to ensure that males from surrounding areas are periodically introduced into the resident population. To simulate the natural selection process, bachelor males should be harvested in preference to territorial individuals. This is in accordance with research indicating that bachelors experience higher mortality and that breeding is accomplished by territorial males.

Opportunities to provision wildlife exist and could be conducted without compromising their wild characteristics. It is generally recognized that the health of wildlife is reduced in the dry season by inadequate amounts of water, mineral salts and digestible energy. It may prove feasible to implement a rotational grazing system by restricting wildlife from selected fenced areas during the wet season. It would be necessary to fence primarily upper slopes and hilltops, since these areas favor those grass species which maintain forage quality in the dry season. These protected rangelands would provide nutritious hay to herbivores during a period when diet quality is generally low. Monitoring of body condition of harvested animals would indicate when these supplemental areas should be accessed. Salt blocks and pumped water could be used to offset deficiencies in natural supplies and attract animals to underutilized areas.

Knowledge of ungulate habitat preferences (Chapter 5) and the biophysical resources existing on WRR (Chapter 2), offer management the ability to regulate animal numbers to available resources. Competent range managers could periodically evaluate range condition and trend for each habitat type, and then modify the cropping regime to ensure an optimal combination of herbivores.

Monitoring seasonal trends in adipose reserves would suggest periods when the harvest of each species should be greatest. Ecological separation of the ungulate community across the topographic gradient ensures that body condition fluctuations for each species are not highly synchronous (Chapter 7). For example, Thomson's gazelle did not maintain fat reserves as long into the dry season as did Grant's gazelle. Thomson's gazelle exploited the early floral greenup along hilltops whereas Grant's gazelle benefitted from residual soil moisture in depressions and a dependence on dicots as dry season forage. In terms of carcass characteristics, it is desirable to harvest populations prior to periods of major weight loss.

9.2 Consumptive Use of Kenya's Wildlife - The Future

A more enlightened attitude is developing among both the public and private sectors that land-use systems utilizing native herbivores can 1) offer Kenya new meat industries and 2) help restore damaged rangelands. Yet, definitive statements on the environmental and economic advantages of game ranching must await decades of scrutiny. For these reasons, it would be a disservice to justify the concept based on the first three years of WRR's existence. It would be equally unfair to condemn any new land-use system because it experiences growing pains during its early development. With these reservations in mind, the following comments are offered.

The performance of WRR has silenced many of the critics who questioned the objectives and claims of Hopcraft's game ranching proposal. Given WRR's present monopoly position of producing quality venison for specialty markets, there is little doubt as to its economic viability. But what is the potential for wildlife to provide cheap protein in sufficient quantities to help the undernourished people of Kenya? Restrictive government regulations for game ranching ensure legitimacy and discourage all but those entrepreneurs who possess adequate amounts of technological experience, rangeland and risk capital. It is unlikely that there are more than a handful of such people in Kenya who have the necessary resources needed to emulate Hopcraft's system. Should the Kenyan government decide to extensify the game ranching industry, other WRR-like enterprises would almost certainly occur; yet this approach may be ill-suited to other regions.

The very nature of WRR's infrastructure precludes its development at a regional scale. A game proof fence resolves questions of animal ownership, encourages higher ungulate productivity by preventing emigration and provides the closed management system required by ecologists to study plant-animal interactions with precision. However, it is costly and requires a sufficiently spacious area to support a community of herbivores throughout the year. Over much of Kenya's semi-arid and arid regions where wildlife still persist in substantial numbers, populations are highly migratory or inhabit regions consisting of numerous small landholdings. Neither are conducive to erecting a game proof fence; the first because yearlong confinement of animals in areas with seasonal water and forage shortages would greatly reduce carrying capacity and the second because of limited capital and land resources. It is primarily a problem of scale, for small ranches would be unable to generate sufficient revenue from wildlife to justify the high capital costs of killing vehicles, guns, abbatoirs, cooling facilities, etc.

WRR's proximity to Nairobi permits fresh meat deliveries. Since many wildlife areas are not located close to major retail markets, other carcass products, such as dried meat (biltong) and vacuum packed items would need to be emphasized.

Venison in Nairobi presently retails for twice the price of beef and weekly orders regularily exceed WRR's self-imposed production quota. Since WRR has been approached by several mid-East representatives who wish to purchase considerable amounts of Kenyan venison, it would appear that a strong export market exists. If Kenyan officials allow the sale of meat beyond its domestic borders, venison could generate badly needed foreign exchange. Despite these optimistic indicators, it seems reasonable to expect the law of supply and demand to eventually deflate prices as greater amounts of meat come on stream. This being the case, the industry must explore ways to reduce capital investment and operating costs to maintain economic attractiveness.

To commercially exploit wildlife in regions where fencing is logistically or economically impractical, new harvesting systems must be developed which recognize communal ownership of the herd and ensure the fair distribution of revenue back to those people whose land supported the harvested animals. Following is a description of a harvesting system which takes into account some of WRR's limitations when applied to migratory wildlife populations and areas of predominantly small landholdings.

Harvesting would be conducted by private companies who would employ biologists knowledgable in animal census techniques, killing teams consisting of spotlighters, shooters and drivers, butchers for processing the carcasses and a transport team responsible for delivery of animal products to market. Initially, company representatives would approach owners of rangeland inhabited by sufficient wildlife to make a harvesting effort profitable. If landowners were agreeable, biologists would document the numbers, sex ratio and distribution of each ungulate species. Plant community studies would be used to suggest optimal combinations of native herbivores. The data would be used to formulate a harvesting schedule that would allow maximum sustained potential offtake. This proposal would be submitted to the landowners, who would agree to distribute revenue according to the proportions of animals supported on each parcel of land.

Cropping mechanics would be similar to the approach developed by WRR, emphasizing night spotlighting for selective age and sex class animals. The number of killing vehicles, shooters and spotlighters used would depend on projected offtake and the cropping period. Harvested animals would be taken to a mobile abbatoir located central to the harvest area. Animals would be processed, inspected by government officials, weighed and stamped, and carcasses transported in the cool night air to Nairobi for chilling in large cooling units while they await retail. Once the quota had been filled, the cropping company would relocate their mobile harvesting system on the next cropping site. Cropping in remote areas would require meat to be refrigerated, dried or cooked prior to delivery to market outlets.

The appeal of this proposal to landowners is that they receive an economic reward for maintaining wildlife populations without being financially encumbered by the labor, expertise and capital investment required to harvest native herbivores. Therein lies the incentive for these people to conserve wildlife. As a "conservation through utilization" strategy, this proposal should encourage an expansion of wildlife into areas where they are not presently tolerated.

The cropping company would be better able to service loans on such capital investment as vehicles, coolers, abbatoirs, etc. by cropping more frequently than would be possible if restricted to harvesting one wildlife community. For example, the killing vehicles and abbatoirs on WRR are in use for part of one day each week. By increasing economic returns to capital, regular cropping should allow venison prices to compare more favorably with beef. Presently, few Kenyans can afford the luxury of game meat when cheaper alternatives are available.

The success of custom cropping will depend on the ability of the government to ensure professional ethics. To discourage over-harvesting, each company would be required to restrict its cropping to a single eco-region. The company would therefore sacrifice future offtake if they chose to overcrop in the short-term. A government agency would be created to monitor game numbers, enforce offtake quotas, inspect and regulate the marketing of carcasses and ensure a fair renumeration to the landowner. Poaching would be discouraged by requiring all meat that enters the market to be identified by a government stamp. It is proposed that funds for operating this agency would arise from a government tax levied on each cropping company according to carcass weight offtake.

A nation-wide study of Kenya's herbivores (MILA, 1980), recommended the creation of the Kenya Wildlife Corporation (KWC) to initiate and regulate consumptive use of plains game. This directive is consistent with the government's stated goal "to identify the best land uses for specific areas of land" and "to ensure a fair distribution of benefits of those uses" (Anonymous, 1975). Since this time, the government has taken the initiative by permitting Hopcraft to explore game ranching through his pilot project. The socio-economic and ecological performance of WRR during its first three years of existence are now being evaluated by the Kenya Wildlife and Management Department. To encourage harvesting of game on a national scale, Hopcraft has recently submitted a proposal similar to the one outlined above.

The above proposals bear similarity to the Kenya Wildlife Management Project (KWMP), which cropped plains game in the Kajiado District in the 1970's. Most observers attribute its demise to poor public support, irregular supplies of meat and the lack of innovative approaches to processing and marketing game products. Although experiencing set-backs, WRR has won the support of both retailers and consumers by ensuring regular supply, meat quality and adopting flexible approaches to venison marketing.

It would appear that the Kenyan government is now in a position to display cautious optimism and take further steps to a more ecologically sound land-use system in those areas where conventional livestock species are poorly adapted.

9.3 References

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